

## CLADISTIC RELATIONSHIPS AMONG PIMELIINE TENEBRIONIDAE (COLEOPTERA)

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*Abstract.*—The cladistic relationships among Tenebrionidae of the subfamily Pimeliinae (=Tentyriinae of authors) are analyzed based on 84 characters examined over 60 adult tribal or generic level taxa. Features of the mouthparts, coxal articulations, ovipositor and internal female reproductive tract are highly variable and important in determining cladistic topology. Nearly all the characters employed display extensive homoplasy, especially convergence, resulting in relatively low measures of consistency of the cladograms. Deletion of less consistent characters results in loss of cladistic detail, however, without significantly improving overall consistency, indicating that even the least consistent features are cladistically meaningful.

The female reproductive tract, which shows exceptional variation that is strongly correlated with cladistic position, is illustrated extensively. Primitively the female tract comprises a bursa copulatrix and accessory gland without a separate spermatheca, as in some Cnemeplatiini and Pimeliini. Most other Pimeliinae may be placed into one of five clades based on configuration of the female tract. In most members of the cnemeplatiine-stenosine clade a capsular or short tubular spermatheca and a short, saccate gland open into the vagina through a common duct. In the pimeliine clade one to several tubular spermathecae and a tubular gland open independently into the vagina or bursa copulatrix. In several taxa of this clade the spermatheca is poorly defined or absent. The asidine clade is characterized by multiple, long, slender spermathecal tubes which open as a fascicle into the base of the accessory gland duct or into the vagina near the duct. A bursa copulatrix is absent. In the eurymetopine clade multiple, slender, tubular spermathecae are attached serially to the base of the accessory gland duct. A bursa copulatrix is often retained. In the tentyriine clade the bursa is modified to form one to several thick, tapering annulate spermathecal chambers. The accessory gland opens into one of the chambers or into the vagina. A number of tribes or genera, including Zolodinini, Falsomycterini, Boromorphini, Lachnogyini, Anepsiini, Vacronini, Nyctoporini and Cryptoglossini do not fit into any of the major clades, because they either display mostly primitive features or discordant combinations of features from different clades.

The following taxonomic changes are indicated. *Alaudes* Horn is transferred to Cnemeplatiini; Araeschizini and Typhlusechini are synonymized under Stenosini; Falsomycterini, containing *Falsomycterus* Pic and *Pteroctenus* Kirsch, merits recognition as a separate tribe of uncertain relationship; *Boromorphini* (*Boromorphus*) merits tribal status (probably near Caenocrypticini); Platypini is synonymized under Pimeliini; Calognathini and Vansonini should be placed in synonymy under Cryptochilini; Elenophorini should be retained to include *Elenophorus* Latreille, *Megelenophorus* Gebien and *Psammetichus* Latreille; Craniotini is synonymized under Asidini; Epitragini is restricted to its new world components; Old World genera previously placed in Epitragini belong in Tentyriini; Edrotini, Triorophini, Trientomini, Auchmobiini and Trimytini are synonymized under Eurymetopini; *Salax* Guérin, *Trilobocara* Solier, *Megalophrys* Waterhouse, *Eremoeccus* Lacordaire and *Derosalax* Gebien are separated as the tribe Trilobocarini Lacordaire; *Orthonychius* Gebien is a junior synonym of *Trilobocara*. *Pseudothinobatis* Freude is transferred from Thinobatini to Epitragini. *Ascelosodis* Redtenbacher is transferred from Tentyriini to Eurymetopini, *Achanius* Erichson and *Ambigatus* Fairmaire are transferred from Evaniosomini to Eurymetopini. Three genera are removed from Pimeliinae: *Eschatoporis* Blaisdell is transferred from Cryptoglossini to Goniaderini; *Ammophorus* Guérin from Nyctoporini to Scotobiini; and *Phtora* (Germar) mistakenly included in Pimeliinae by Doyen and Lawrence (1979) to Phaleriini.

During the past two decades the higher classification of the family Tenebrionidae has been scrutinized by a number of workers (Watt, 1967, 1974; Doyen and Lawrence, 1979; Tschinkel and Doyen, 1980; Doyen and Tschinkel, 1982), resulting in major changes in the constitution of many tribes and in the arrangement of the tribes into subfamilies (Aalbu and Triplehorn, 1985; Doyen, 1984, 1985, 1989; Doyen et al. 1989; Endrödy-Younga, 1989). However, this work has centered almost exclusively on the tribes in which defensive glands are present or secondarily lost. This group of tribes includes the beetles formerly constituting the families Lagriidae, Alleculidae and Nilionidae, as well as perhaps 10,000 species in about 40 tribes of Tenebrionidae. These beetles generally inhabit relatively mesic environments, including temperate and subtropical grasslands and woodlands. They are especially speciose in tropical forest and savannah habitats. With occasional exceptions they are not particularly diverse in extremely arid habitats, but several tribes, such as Opatrini, Scaurini and Scotobiini, are abundant in subarid environments.

A second group of tribes, comprising the subfamily Pimeliinae (=Tentyriinae of Doyen and Lawrence, 1979; Doyen and Tschinkel, 1982), lacks defensive glands. In addition, all but a single genus of Pimeliinae have the aedeagus rotated 180° about the longitudinal axis, so that the median lobe is dorsal to the tegmen rather than ventral, and all except the tribe Pimeliini lack external membranes between the apical abdominal sternites, as discussed below in greater detail. Members of the Pimeliinae primarily occupy arid or subarid habitats, with many species able to survive even the exceptionally dry conditions of deserts such as the Namib, Atacama and Sahara, where they often form dominant faunal elements in terms of biomass and numbers of individuals (Crawford and Seely, 1987; Koch, 1961; Pierre, 1958).

It is still unsettled whether absence of defensive glands is a synapomorphy for Pimeliinae. If so, absence of glands would represent a secondary loss. Alternatively Pimeliinae could be the sister taxon to all other Tenebrionidae, in which case absence of glands would be primitive, since outgroup taxa lack glands. One bit of distributional evidence which suggests secondary gland loss is the almost complete absence of Pimeliinae from the Australian region. This absence could indicate that Pimeliinae are younger than most of the other major lineages, in which glands are present. A complicating difficulty is the fact that defensive glands have clearly arisen at least twice in Tenebrionidae (Tschinkel and Doyen, 1980). These problems have been addressed in earlier investigations (Watt, 1974; Doyen and Tschinkel, 1982), but need to be reevaluated in light of recent evidence, especially regarding the bauplan of Pimeliinae.

In Pimeliini and Platypopini the membranes between abdominal sternites five to seven are exposed, whereas in all other pimeliine tribes they are concealed. This variation has been interpreted as evidence that Pimeliinae might be polyphyletic (Doyen and Lawrence, 1979). Watt (1974, 1992) favored a monophyletic origin of Pimeliinae, and this view is supported by the present study, which indicates that the abdominal membranes are secondarily exposed in Pimeliini, as detailed below.

The name Tentyriinae is used in recent catalogs to refer to the beetles here termed Pimeliinae; the informal 'tentyrioid lineage' was used in the same sense (Doyen and Lawrence, 1979; Doyen and Tschinkel, 1982). Pimeliinae has clear priority (Watt, 1974, 1992) and was employed by Doyen et al. (1989).

In number of tribes and species, Pimeliinae comprise nearly half the Tenebrionidae

and the external body form of adults is extremely variable. Nevertheless, larval morphology and the adult characters mentioned above indicate that Pimeliinae comprise a single lineage. Consequently, in all previous analyses they have been represented by a few exemplars, with no attempts to depict relationships among the tribes. The intent of this paper is to survey the morphological variation among adult Pimeliinae and to make initial estimates of the cladistic structure of this subfamily.

#### LIMITS OF PIMELIINAE

The old pimeliine tribes Zopherini and Dacoderini were previously removed from Tenebrionidae (Watt, 1967, 1974; Doyen and Lawrence, 1972). A number of tribes or genera have been moved into Pimeliinae from other lineages of Tenebrionidae. These include Coniointini, Branchini, Physogasterini, Praocini (Doyen, 1972) Varonini, Cnemeplatiini, Falsomycterini, *Psammotichus*, *Boromorphus* (Doyen and Lawrence, 1979) and *Zolodinus* (Doyen et al., 1989). The systematic importance of the last had been recognized by Watt (1974), who placed it, along with *Tanylypa*, in his subfamily Zolodininae. As discussed below, the affinities of *Zolodinus* and related genera are still somewhat uncertain. *Bius*, tentatively placed in Pimeliinae by Watt (1974) belongs in Tenebrionini (Doyen, 1989). Besides those mentioned above, only a few genera are improperly included in Pimeliinae in present catalogs. *Eschatoporis* Blaisdell is listed under Cryptoglossini in both catalogs by Gebien (1910, 1937), that by Leng (1920) and in the checklist by Papp (1961), despite the clear original placement in or near Scaurini (=Eulabini of Berry, 1973) by Blaisdell (1906: 76). There appears to be no published explanation of the transfer into Cryptoglossini, and, strangely, Blaisdell himself never commented on this catalog position which is so different from his original placement.

Examination of specimens in the California Academy of Sciences has revealed that Blaisdell was also incorrect in his assessment of this peculiar genus, which lacks eyes and has been found only in caves or in fissures in rocky, porous soil. The features he lists as shared with Eulabini (e.g., small mentum, antennae 11-jointed, abdomen with external membranes between apical segments, etc.) are without exception plesiomorphies distributed very widely among non-pimeliine Tenebrionidae. Probably the general similarity in body shape shared by *Eschatoporis* and some Eulabini influenced Blaisdell's placement, because none of his characters are diagnostic at the tribal level.

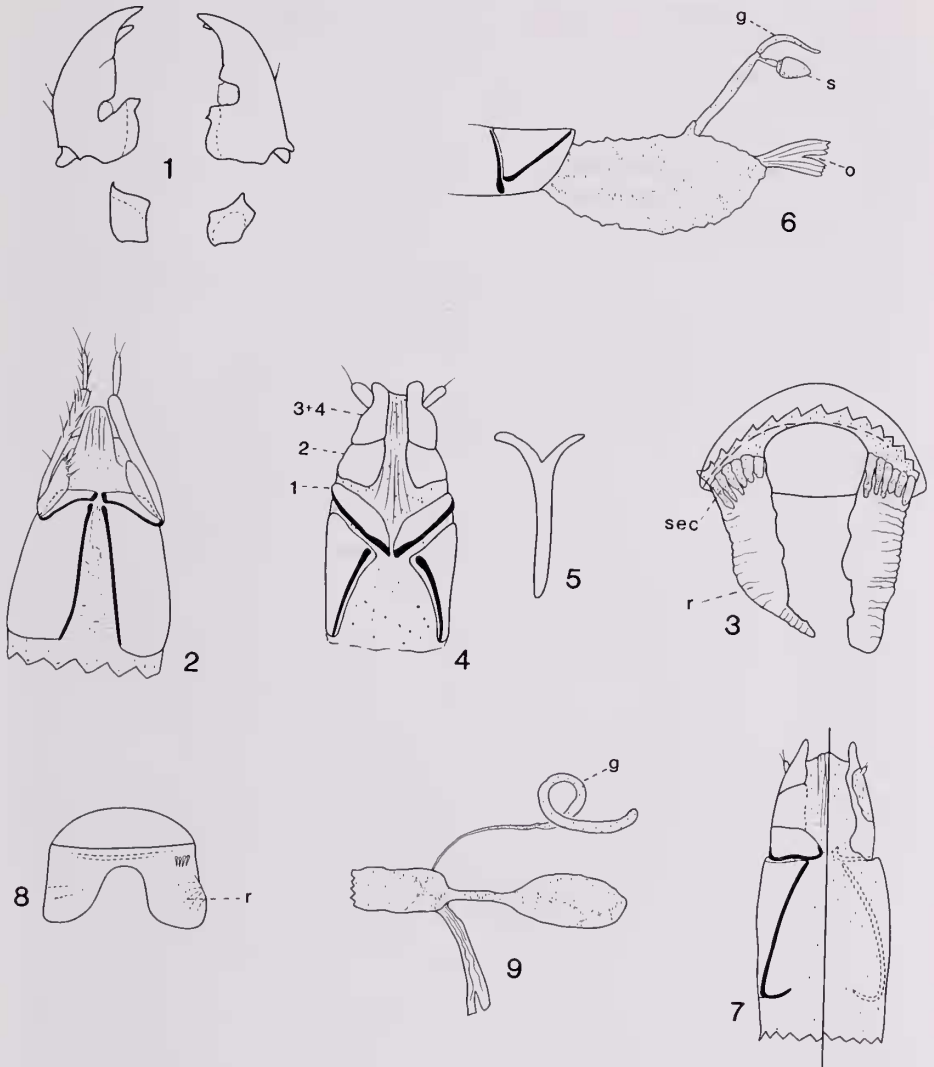
Because of the rarity of this beetle complete dissections have not been made, but it has been possible to examine the mouthparts, ovipositor and some internal features, which all indicate that *Eschatoporis* belongs in Lagriinae. The most important characters include: 1. Defensive glands absent (but abdominal sternites with external membranes); 2. Seventh abdominal sternite (fifth visible sternite) with distinct groove around posterior inner margin; medially the posterior margin is weakly but distinctly subangulate; 3. Elytra with 10 striae; 4. Labrum subquadrate; 5. Mandibles elongate, with long, highly asymmetrical molar lobes (Fig. 1); 6. Ovipositor with large, digitate gonostyli and elongate, subdigitate apical coxite lobe (Fig. 2). Among Lagriini defensive glands are absent in Goniaderini, some Lupropini, Laenini, Cossyphini and Belopini. Belopini and Cossyphini have the abdominal membranes internalized and

are specialized in other characters as well (Doyen and Tschinkel, 1982). Lupropini, Laenini and Goniaderini are closely related, with confusing distributions of characters (see discussion in Doyen et al., 1989). Nearly all the genera in these tribes lack the tentorial bridge, which is present in *Eschatoporis* and *Anaedus*, but presence of the bridge is plesiomorphic. The configuration of the ovipositor of *Eschatoporis* is distinctly lagrioid but not obviously very similar to those of *Anaedus* or other members of these tribes. The transverse basal coxite lobes with short longitudinal baculi and oblique second lobes are autapomorphous. The basal coxite lobes in *Adelium* are short and transverse, but the baculi are also transverse. In addition, *Adelium* has large defensive glands and differs in other features. *Eschatoporis* is here placed in Goniaderini, recognizing that future changes may be required when larvae and other internal features, especially the female reproductive tract can be examined.

*Ammophorus* Guérin, with about a dozen species in western South America, the Galapagos Islands and Hawaii, was originally placed in Nyctoporini (Lacordaire, 1859), along with *Eulabis* and *Epantius*. The last two were removed by subsequent workers, but *Ammophorus* remains in Nyctoporini in all current catalogs and checklists. Even superficial examination reveals that *Ammophorus* has external membranes between the apical abdominal sternites which removes it from Pimeliinae. The defensive glands are long, saccate and without common volume (Fig. 3). The reservoir walls bear circular wrinkles, but are not truly annulate. The secretions appear to drain through a line of basal ducts. The ovipositor (Figs. 4, 5) has short proctiger lobes and three distinct coxite lobes, with large, lateral gonostyli. The internal female tract (Fig. 6) consists of a saccate vagina bearing a single diverticulum which is apically branched. The tubular branch appears to be the spermathecal accessory gland and the capsular, ovoid structure the spermatheca. The aedeagus is unremarkable except that the median lobe is atrophied.

The configuration of the defensive reservoirs (Fig. 3) is similar to that of Opatrini (sensu lato), except that the reservoir bases are usually constricted in the latter, which also have a very different female tract, typically with a long, thin, tightly coiled spermatheca. *Ammophorus* is similar in body form to Eulabini, which also have short proctiger lobes on the ovipositor. However, in Eulabini the spermatheca again is long, slender and tightly coiled and the defensive reservoirs are very short and eversible, similar to those in *Neatus* and *Zophobas*. *Ammophorus* is also phenetically similar to Scotobiini, particularly to some species of *Scotobius*. *Scotobius* has a short proctiger lobe, but the apical part of the ovipositor is configured differently than in *Ammophorus*. In addition, *Scotobius* has short saccate glands which have the appearance of being eversible, and has a thick coiled spermatheca and long, slender gland. Despite these differences, Scotobiini and *Ammophorus* share a peculiar synapomorphy first noticed by Medvedev (1977) in *Scotobius*—namely, the presence on the truncate apex of the last antennomere of clusters on dome-shaped placoid sensoriae. These are readily visible under higher magnifications of a dissecting scope, and a few are also visible on the rims of the preterminal antennomeres. On the basis mainly of this character, *Ammophorus* is here referred to Scotobiini. It should be pointed out that large, placoid sensoriae also occur in Ulomini, which do not differ radically from Scotobiini in the other characters discussed above, but have very elongate defensive reservoirs with little common volume (Tschinkel, 1975a). In ad-





Figs. 1-9. Features of taxa removed from Pimeliinae. 1. *Eschatoporis nunenmacheri*, mandibles (dorsal) and molar lobes (medial); 2. Same, ovipositor, ventral; 3. *Ammophorus insularis* Boheman, abdominal defensive reservoirs, dorsal; 4. Same, ovipositor, ventral; 5. Same, spiculum ventrale; 6. Same, internal female reproductive tract; 7. *Phtora fossoria* Wollaston, ovipositor, ventral and dorsal; 8. Same, defensive reservoirs, dorsal; 9. *Phtora millingeni* Reitter, internal female tract. g = accessory gland; o = oviduct; r = reservoir; s = spermatheca; sec = secretory tissue of defensive gland; 1, 2, 3, & 4 = lobes of coxite.

dition, larvae of Ulomini mostly occur in old rotted wood, rather than soil, where scotobiine larvae are found (Cekalovic and Quezada, 1973). Larvae of the ulomine, *Eutochia*, inhabit soil (St. George, unpubl.; W. Steiner, pers. comm.), however, and have the ninth abdominal tergite configured much as in Opatrini (s.l.) rather than enlarged and paraboloid, as in Ulomini. These larval features, together with the unusual antennal sensoriae shared by Ulomini and Scotobiini, suggest that the possibility of a close relationship be examined more closely.

*Phtora* Germar (nec Mulsant)(=*Cataphronetis* Lucas; see Spilman, 1966) was transferred into Pimeliinae by Doyen and Lawrence (1979) on the basis of misidentified specimens. The apical abdominal sternites in *Phtora* are separated by distinct external membranes, defensive reservoirs are present and the aedeagus is in the normal (non-inverted) orientation, clearly excluding this genus from Pimeliinae.

Lacordaire placed *Phtora* (as *Cataphronetis*) in his Ulomides, which it resembles in general body form and in having the seventh abdominal tergite partially exposed and pygidiform. *Phtora* differs from all Ulomini in the form of the ovipositor, the defensive reservoirs and the structures of the internal female reproductive tract. The ovipositor is broad, with the coxites about  $\frac{1}{4}$  times longer than the paraprocts (Fig. 7). Lobing of the coxite is somewhat obscure, but there appear to be four divisions, the apical being sclerotized and prong-shaped. The gonostyles, small but distinct, are markedly preterminal. The defensive glands are short-saccate without annular folding or thickening and with large common volume (Fig. 8). Each reservoir is bent slightly laterad toward its apex. The secretion collecting ducts are arranged in a basal line. The female reproductive tract (Fig. 9) consists of the vagina, constricted before the saccate bursa copulatrix, and a single diverticulum, non-glandular in its basal half, gradually enlarging to the glandular apical half.

In Ulomini the ovipositor generally is configured as in *Phtora*, with coxites and paraprocts of approximately equal length, but the gonostyles are terminal (*Eutochia*) or slightly preterminal (*Uleda*, *Uloma*). The defensive reservoirs are large and very elongate, with little common volume. The female tract includes both spermatheca and accessory gland, which open into the end of the vagina, without a bursa copulatrix.

The only taxon which is similar to *Phtora* in all the features cited above is Phaleriini (Tschinkel and Doyen, 1980: figs. 10, 27). The ovipositors of *Phaleria* species are generally configured as in *Phtora*, including markedly preterminal gonostyles. The internal tract of *Phaleria* has a large bursa set off from the vagina by a distinct constriction and has secretory cells only along the apical half of the gland diverticulum. Both the common oviduct and the accessory gland open into the vagina basad of the constriction, as in *Phtora*. The broad, flattened fore tibiae with spinose posterior surface; the slightly exposed, pygidiform seventh abdominal tergite; and the wing configuration (long membrane; small recurrent cell circumscribed by thick veins) are obvious external similarities between *Phtora* and Phaleriini. In addition, both have compound sensoriae on the inner and outer angles of the apical four or five antennomeres. Other basal members of the Diaperine lineage, such as *Corticeus* have the spermatheca differentiated as an enlarged saccate or capsular structure and have the apical lobes of the coxites digitate with gonostyles inserted terminally (Tschinkel and Doyen, 1980). Finally, *Phtora* is a soil inhabitant, where it is found beneath dry dung and stones (Lacordaire, 1859). Most records suggest oasis or littoral habitats; Phaleriini are restricted to seacoasts, mostly to sandy substrates.

Because of the preponderance of evidence *Phthora* is transferred into Phaleriini. I predict that larvae, when associated, will substantiate this placement.

#### MATERIALS AND METHODS

The analytical portion of this study is limited to adults. Larvae of at least 50 species of Pimeliinae have been associated with adults and described (Keleynikova, 1963, 1970, 1976; Marcuzzi and Rampazzo, 1960; Marcuzzi et al., 1980; Aalbu, 1985; Artigas and Brañas-Rivas, 1973; Brown, 1973; Costa et al., 1988; Doyen, 1974; Ghilarov, 1964; Schulze, 1962, 1964, 1974; Skopin, 1959, 1960; Watt, 1974). Nevertheless, most of these belong to a few tribes, principally Asidini, Coniointini, Tentyriini, Akidini, Pimeliini and Adesmiini. Several other tribes are known from a single larval association (e.g., Stenosini, Cnemeplatiini, Erodiini, Vacronini), while about half are undescribed as immatures (e.g., Falsomycterini, Araeoschizini, Typhlusechini, Ceratanisini, Cryptochilini, Lachnogyini, etc.). Where larvae are well enough known to influence classifications, the pertinent information is considered in the taxonomic discussions, but larval characters do not appear on the cladograms.

In order to examine internal features adults were softened in hot water, partially dissected, and then soaked overnight in cold 10% KOH. Mouthparts (and entire bodies of very small species) were preserved in glycerine on depression slides. Wings were dried in the expanded position on microslides and protected with coverslips. Internal female reproductive tracts were stained in chlorazol black and stored in glycerine on depression slides. Dissection methods were described in greater detail by Tschinkel and Doyen (1980).

Characters and character states were tallied for 148 genera, each represented by one or more species. These included all the tribes recognized by Gebien (1937, 1938–42) except Gnathosiini, Remipedillini and Leptodini, which were unavailable. For small tribes all or most of the genera were included. For large, diverse tribes a selection of genera, ranging from those appearing to have large numbers of plesiomorphic characters to those with many derived character states was examined. Critical characters, especially of the female reproductive tract, were sometimes examined without full dissections.

A conspectus of tribes and genera studied appears in Appendix I. Hierarchically the tribal level was used as the primary unit for cladistic analysis. This was necessary because the large number of genera would have enormously increased computation time. For each tribe the genera were scanned to determine the most primitive state present, which was used to construct a tribe by character matrix (Appendix III). In addition to the tribes listed in Appendix I, a number of genera were included as OTU's. These were either taxa which preliminary analysis showed not to fit well into existing tribes (e.g., *Salax*, *Trilobocara*) or whose position in current classifications is problematic (e.g., *Elenophorus*, *Megelenophorus*, *Boromorphus*, *Anchomma*, etc.). The tribe Asidini was represented by 4 OTU's, corresponding to the geographical regions of occurrence. The resulting matrix measured 84 characters by 60 OTU's (including Zolodinini)(Appendix III).

Cladistic computations were done with HENNIG86 by J. S. Farris. Cladograms were derived using three different outgroups, because the sister to Pimeliinae is uncertain. 1. *Zolodinus* as outgroup. Watt (1974: 19) proposed that *Zolodinus* is the

sister to Pimeliinae, based primarily on the lack of defensive glands and external abdominal membranes and the inverted aedeagus. Doyen and Tschinkel (1982) and Doyen et al. (1989) have pointed out some difficulties with accepting the sister status of *Zolodinus* and Pimeliinae, and these are explored below. 2. Belopini as outgroup. Adult Belopini share some features such as concealed abdominal membranes with Pimeliinae, even though characters of larvae clearly show that they are derived Lagriinae (Doyen, 1988). 3. Hypothetical outgroup. This character set consists of primitive states for every character.

The commands "mhennig\*" and "bb\*" were used to calculate trees, because the command "ie" did not terminate. The input sequence of the OTU's was repeatedly altered to avoid artifacts resulting from ordering (Griswold, 1993).

#### CHARACTERS AND CHARACTER STATES

Primitive members of several pimeliine lineages are winged (most Epitragini, Vacionini, some Cnemeplatiini, Eurymetopini, Tentyriini, Trilobocarini) but the great majority of these beetles are flightless, often with strongly altered body forms. Frequently the pterothoracic region is highly modified, with the metathorax reduced and the metendosternite fused with the mesocoxal cowlings and/or the mesotergum. The elytra are joined to one another and to the abdominal sternites by virtually immobile tongue and groove joints. These types of modifications and others such as fusion of the prothorax with the pterothorax, reduction of the abdomen or constriction of the pro-mesothoracic junction have produced highly distinctive body forms which characterize many genera and tribes of Pimeliinae. For example all Erodiini have subspherical bodies with the prothorax fused to the hind body, the head enlarged and the foretibiae flattened with serrate outer margins. This general body form represents a set of adaptations for life in unconsolidated sand and occurs in several other tribes of Pimeliinae (e.g., some Coniontini, Edrotini, Adesmiini) as well as several other subfamilies of Tenebrionidae. Other notable body forms include: 1. A strongly flattened, subcircular body with sharply explanate margins, as in many Eurychorini and some Zophosini. The flattened body appears in some cases to be an adaptation for allowing quick entry into the loose sand in which these beetles live and Koch (1955) referred to these beetles as sanddivers. 2. A moderately flattened body with reduced, narrow abdominal venter strongly interlocked with the metathorax. The elytra are expanded laterally far beyond the abdominal sternites and the metacoxae are strongly oblique. This body form is unique to the Zophosini, which are extremely active, diurnal beetles whose rapid and erratic escape behavior may be compared to that of Gyrinidae. Koch (1955) referred to them as sand-jumpers. 3. An elongate subcylindrical body with more or less strong constriction at the pro-mesothoracic joint. The lateral pronotal carinae are often obsolete or absent and the antennae are often moniliform. This general body form occurs in Elenophorini, Stenosini, Araeoschizini and some Tentyriini and Eurymetopini. Apocryphini is a comparable form in the group of Tenebrionidae with defensive glands. Larger beetles with this body form are apparently unspecialized ambulatory insects. Very small beetles with similar form are often described as ant-like and many Stenosini and Araeoschizini are myrmecophilous. The functional significance of the body configuration is unclear, however.



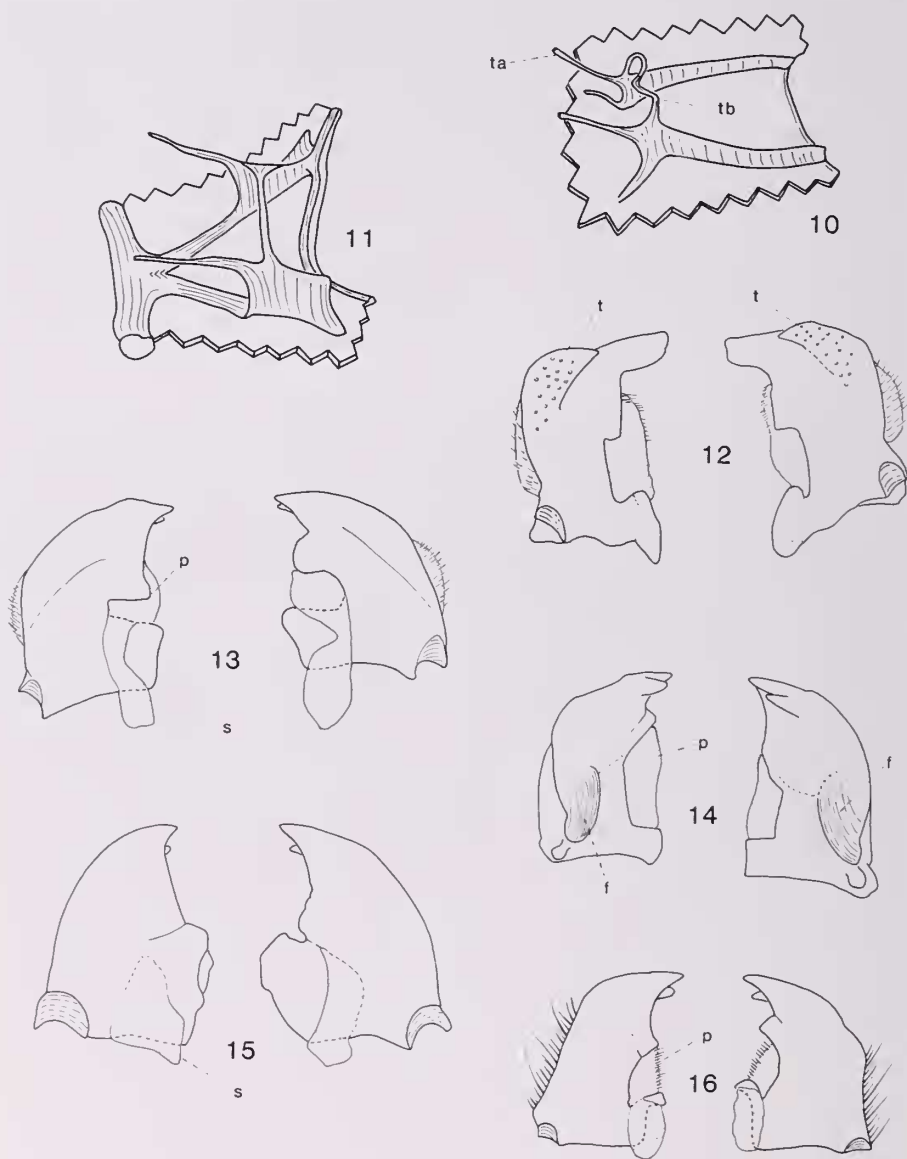
As implied above, similar body forms occur repeatedly in Pimeliinae, and such similarities appear to be exceedingly common when individual characters are considered. In some instances similarity is clearly the result of convergent adaptations for similar styles of life. In many other instances, however, it is unclear whether they represent synapomorphies or convergences. For example, *Elenophorus* (Mediterranean area) and *Megelenophorus* (southern South America) both with the waisted body form described above, share many other morphological characteristics, such as large body size, very long legs, inflated elytra with strong lateral costae, very long third antennal segment and clypeus with deep lateral emarginations. However, many of these features are also shared with *Psammotichus* (South America) and Akidini (Mediterranean-Asian). Since vicariance between the Mediterranean region and South America is not common, one might suspect that the similarity between *Elenophorus* and *Megelenophorus* is the result of convergence.

Similar problems attend the interpretation of numerous characters of Pimeliinae, such as the enlarged mentum, the dorsolateral teeth on the mandibles, closure of the mesocoxal cavities by the sterna rather than the epimeron, moniliform antennae, etc., and together with strong autapomorphism have stood as the major obstacle to defining relationships among the pimeliine tribes. Interpretation of homology and polarity of characters is discussed below, but in general all similarities were initially regarded as synapomorphies and distribution of derived states on the cladograms was considered as confirmation or rejection of homology.

Character states were coded as graded series whenever possible, with divergent states at opposite extremes of the scale. The resulting character state trees may be derived from Appendix II. A few characters, for which several divergent states were present, were treated as non-additive. Character polarity was established either by using Zolodinini or Belopini as outgroup, or by treating all non-Pimeliinae as the outgroup. For the latter case, used to create a hypothetical outgroup, character states occurring commonly among the non-pimeliine tribes were considered primitive.

**Endocranial skeleton (Characters 0-8).** The primitive configuration of the tentorium is similar to that of *Tenebrio* (Doyen, 1966: fig. 9; Doyen and Tschinkel, 1982: fig. 1), with a simple, transverse bridge connecting the laminar posterior arms. The bridge is absent in all Asidini and Craniotini, and absent or incomplete in members of several other pimeliine tribes, including Epitragini, Tentyriini and Eurychorini. The tentorial bridge is also lacking in some non-Pimeliinae, principally certain tribes of Lagriinae (Doyen and Tschinkel, 1982). A strongly arched bridge (Char. 5), characteristic of the subfamily Diaperinae, occurs among Pimeliinae only in the genus *Araeoschizus* (Doyen and Lawrence, 1979: Fig. 33). The bridge is modestly arched and bent anterad (Fig. 10) in scattered taxa in various genera, and in a few others is much thickened (Doyen and Lawrence, 1979: Fig. 32) (Char. 2). Neither of these states is synapomorphic at the tribal level, however, and neither appears in the cladograms.

Size (Char. 3) and position (Char. 4) of the tentorium vary in only a few taxa. The tentorium is relatively small in Cnemeplatiini and Araeoschizini. In the latter the tentorium is located midway between the oral and occipital foramina, rather than close to the occipital, as in all other Tenebrionidae. This suggests that reduced size has evolved convergently in the two groups. In Zophosini the posterior arms of the tentorium continue anterad as low ridges meeting just behind the submentum (Char.



Figs. 10-16. Tentoria and mandibles. Tentoria of: 10. *Alaephus pallidus* LeConte; 11. *Zophosis testudinaria* Fabricius. Mandibles of: 12. *Himatismus* species (Thabazimbi, Transvaal), dorsal; 13. *Asida alaudi* Serville, dorsal; 14. *Aryemnis* species (Santa Cruz, Bolivia), ventral; 15. *Zophosis testudinaria*, dorsal; 16. *Lepidocnemeplatia sericea* (Horn), dorsal. f = ventral fossa; p = prostheca; s = submola; t = dorsal tooth; tb = tentorial bridge.

6; Fig. 11). Similar ridges in the more derived genera of Adesmiini are not confluent and are regarded as representing convergence. The tentorium is open between the bridge and the gula (Char. 7) in all but a few Anepsiini.

An endocranial dorsomedial septum (Char. 8) occurs only in Edrotini and Cryptochilini, and does not appear as a synapomorphy in the cladograms. No functional significance can be assigned to any of these endocranial skeletal features.

**Mandibular and labral configuration (Characters 9-14).** A characteristic feature of the mandibles of many Pimeliinae is a tooth on the dorsolateral margin (Chars. 9, 10; Fig. 12). The tooth, which is usually at about the middle of the mandible, varies greatly in size and prominence among different genera and tribes. Typically the tooth is larger on the right than on the left mandible (teeth subequal in Fig. 12), sometimes occurring only on the right. Mandibular teeth are present in diverse Eurymetopini, Trimytini, Tentyriini and related tribes, where they are apparently a primitive feature, lost in some genera. They are uniformly absent in the asidine group of tribes (Fig. 13).

The dorsal mandibular teeth are often described as clasping the labrum, but actually they are adjacent to or sometimes slightly overlapping the labrum at rest, without gripping it. Large, overlapping teeth might serve a protective function by securing the labrum which closes the opening between the mandibles, but this would not seem a likely function when the teeth are very small. It is also unclear why the right tooth is often much larger than the left.

Apomorphic states of Characters 12 to 14 are restricted to single tribes or portions of tribes. Character 12 refers to a deep cavity near the ventral articulation of the mandibles of Evaniosomini (Fig. 14). A similar cavity occurs in *Cnemodinus*. Character 14, State 1 refers to the mandibular configuration of Zophosini (Fig. 15), where the retinaculum is subadjacent to or contiguous with the molar lobe and the prostheca is very narrow and transverse or absent between prostheca and mola. A similar configuration occurs in some Molurini. In a few genera such as *Trilobocara* the prostheca is entirely absent (Char. 13) but this is not a synapomorphy in any of the cladograms. In *Lepidocnemeplatia*, *Actizeta*, *Alaudes* and *Thorictosoma* the contact area of the molar lobe is reduced, in *Lepidocnemeplatia* and *Actizeta* to a punctiform or narrowly transverse prominence (Fig. 16)(Char. 14, State 3).

In lagriine tenebrionids the labrum is elongate, the primitive condition. Watt (1974) listed Pimeliinae as having the derived state (labrum much wider than long). However, in a number of Pimeliinae, including Epitragini, Thinobatini, Edrotini and Trimytini the labrum is subquadrate, or slightly longer than broad, which was coded as primitive in the following analyses. Nevertheless, in the cladograms the subquadrate labrum appears as a reversal in the tentyriine lineage. Thus, the primitive condition of this feature in Pimeliinae is not clear.

**Form of maxilla, labium and labrum (Characters 15-28).** Structure of the maxilla is relatively uniform throughout Tenebrionidae, the principal variation involving the form of the lacinia, which may be simply setose or may bear a coarse spine or uncus (Char. 15). The latter state was considered primitive by Doyen and Tschinkel (1982), as it is here. A bispined uncus is considered independently derived. However, it must be emphasized that variation in this character is confusing. Many tribes have the uncus either present or absent in different genera, and a distinct uncus is probably easily evolved by enlargement of one of the maxillary setae.

Characters 16 to 21 and 28 describe the articulatory region of the ventral mouthparts. Primitively in Pimeliinae, as in other Tenebrionidae, the maxillary articulations are exposed lateral to the labium (Fig. 21). In contrast, in many Pimeliinae the mentum is enlarged and subadjacent laterally to the large, forward projecting subgenal processes (Figs. 22–24), concealing at least the basal portion of the maxillae. The latter condition is obviously derived, and has been used in classification. Differences in details of structure, however, indicate that enclosure of the maxillae has occurred several times independently, and this is shown on the cladograms, as well. Moreover, in some tribes, such as Asidini, a range of conditions exists from primitive to derived.

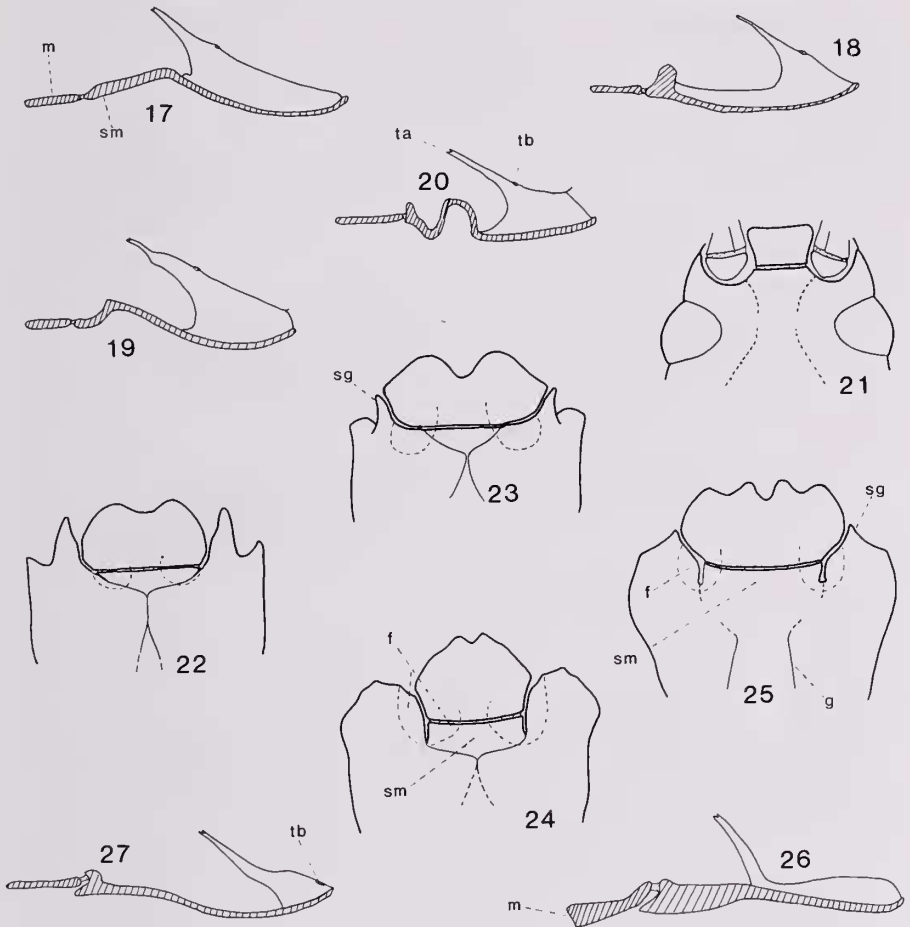
In all Pimeliinae in which the maxillary bases are concealed, the posterior rim of the oral foramen becomes thickened and inflexed (Char. 28; Fig. 18), forming a marginal ridge to which the ventral mouthparts are articulated. The thickening may occur only behind the cardines, or may extend medially, forming a continuous ridge between the cardinal sockets. In many tribes, such as Eurymetopini and Tentyriini both conditions exist with intermediates. These tribes were coded with the primitive state. In most taxa the postoral region is flat or nearly so, but in a few, such as Triorophini, the oral rim is everted so that it appears elevated in relation to the ventral head capsule (Fig. 19). In *Edrotes* and a few others the submentum becomes invaginated as well (Fig. 20). These modifications appear to rigidify the head capsule, as well as provide a means for concealing the maxillary articulations.

Maxillary base concealment occurs by formation of large internal sockets for the cardines (Char. 16). The sockets may be located principally on the inner surface of the submentum, as in Epitragini and Adesmiini (Fig. 22), on the inner surface of the subgenal processes, as in the Zophosini and Eurychorini (Fig. 23), or in both, as in Eurymetopini, Tentyriini (Fig. 24), and several other tribes. In these forms the subgenal processes are closely contiguous with the submentum and at least the basal part of the mentum (Char. 20). In many Asidini the subgenal processes are subadjacent to the mentum, but in several Nearctic (*Asidopsis*, *Heterasida*) and Neotropical (*Cardigenius*, *Scotinus*) genera the subgenae and mentum are separated by an appreciable gap, and many intermediate conditions exist (see Brown, 1971; Figs. 14, 19, 25, 26). The proportion of the mentum which is in contact with the subgenae also varies, as do other structural details (see below), suggesting that enclosure of the ventral mouthparts has occurred several times independently. The joint between the submentum and gula (Char. 21) is almost always rigid, but is flexible in a few taxa such as Erodiini, Calognathini, and Praocini. A rigid joint is present in nearly all non-Pimeliinae, and it seems certain that the flexible condition is derived.

In most Pimeliinae the submentum remains as a distinct sclerite (Figs. 22–24), as in most other Tenebrionidae (Char. 18). In a few, such as *Edrotes*, the submentum is fused to the gula without trace of a suture (Fig. 25). In Akidini and in South African Asidini the submentum is greatly reduced and not visible externally. In most species the submentum is produced between the cardinal sockets as a pedicel (Char. 19) against which the mentum is hinged (Figs. 24, 25), and this is the condition in non-Pimeliinae. In a few taxa (e.g., Zophosini, Coniontini, some Eurychorini, etc.) the submentum is essentially flat between the sockets (Fig. 23). There is no obvious correlation between maxillary concealment and the development of the submentum, and the significance of the pedicellate and nonpedicellate states is not clear.

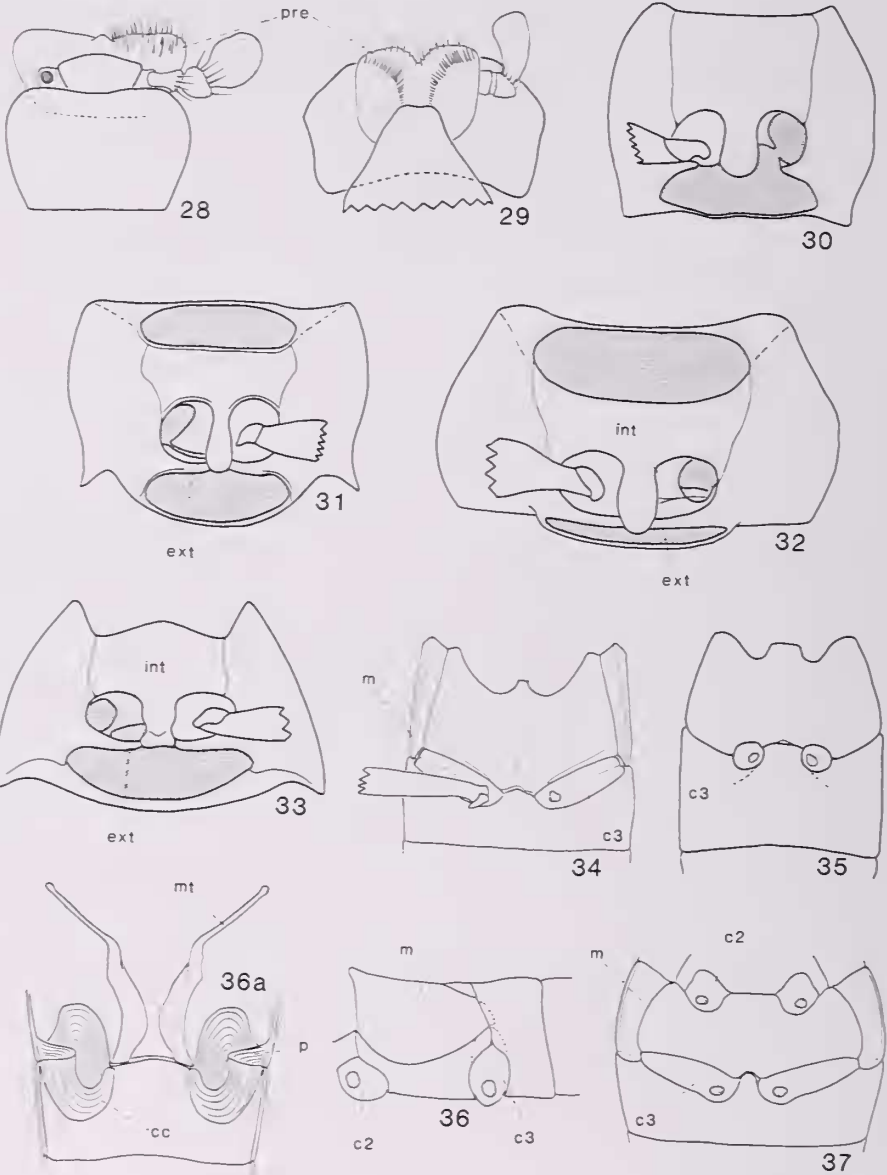
The shape of the mentum varies from subquadrate to transversely elongate, with





Figs. 17–27. Structural features of the oral region. Parasagittal sections (diagrammatic) of the postoral regions of: 17. *Zolodinus zealandicus* Blanchard; 18. *Zophosis (Gyrosis) orbicularis* Deyrolle; 19. *Chilometopon pallidum* Casey; 20. *Edrotes ventricosus* LeConte. Ventral aspects of postoral regions of: 21. *Eupsophulus castaneus* Horn; 22. *Adesmia chiyakensis* Kuntzen; 23. *Zophosis testudinaria*; 24. *Auchmobius sublaevis* LeConte; 25. *Edrotes ventricosus*. Parasagittal sections of: 26. *Eurychora barbata* Olivier; 27. *Vansonium bushmanicum* Koch. f = fossa for cardo; g = gular suture; m = mentum; sg = subgenal process; sm = submentum; ta = tentorial arm; tb = tentorial bridge (absent in *Eurychora*).

the anterior border either truncate to slightly emarginate or deeply concave or notched. These characters (25, 26) are easily polarized by comparison with non-Pimeliinae. The basal articulation of the mentum to the submentum is an external hinge (Figs. 17–20) in most taxa (as in non-Pimeliinae). In Eurychorini and Stenosini the base of the mentum is greatly thickened, with the hinge concealed beneath the submentum (Figs. 26, 27).



Figs. 28-37. Selected structural features. 28. Labium of *Zolodinus zealandicus*, ventral; 29. Labium of *Omopheres ardoini* Kulzer, dorsal; 30. Prothorax of *Zolodinus zealandicus*, coxal cavities internally open; 31. Same of *Lepidocnemeplatia sericea*, coxal cavities very narrowly open internally; 32. Same of *Pachychila intermedia* Haag, showing tentyrine style of internal closure; 33. Same of *Asida servillei* Solier showing asidine style of closure; 34. Metacoxal region (ventral) of *Eupsophulus castaneus*, showing metacoxal closure by attenuate metepimeron; 35. Same. *Alaudes singularis* Horn, closure by sternites; 36. Same (lateral), *Pachynotelus albonotatus* Haag, closure by sternites, metepimeron broadened; 36a. *Pachynotelus*, internal view of me-

The prementum is fully exposed and membranous or very lightly sclerotized (Chars. 22, 23) in a few Pimeliinae such as *Zolodinus* (Fig. 28). This condition is common to many non-Pimeliinae, and is undoubtedly the primitive state. In the derived state, present in most Pimeliinae, the prementum is largely retracted beneath the mentum (Fig. 29), and typically has a pair of basal sclerites. In a few taxa, such as Asidini, the entire prementum becomes strongly sclerotized. Primitively the prementum is subequal in width to the mentum, as in non-Pimeliinae, but in the great majority of pimeliines the mentum is much broader than the prementum.

The function of most of these ventral mouthpart modifications is probably defensive. Internalization of membranes and articulations has occurred repeatedly in Pimeliinae, and probably decreases vulnerability to suctorial feeders such as arachnoids, which are among the principal predators of arid land tenebrionids. I have observed solpugids unsuccessfully probing with the chelicerae around the highly modified mouthparts of *Edrotes*. In contrast they quickly penetrate the oral region of *Eusattus* of similar size, where the maxillae are exposed. The operculate closure of the oral opening may also be important in water conservation.

**Procoxal cavity closure (Characters 30-32).** Closure of procoxal cavities may be either external or internal (Figs. 30-33). External closure is derived through a ventral extension of the notum as the postcoxal bridge (Doyen and Tschinkel, 1982: Fig. 21). Internal closure is derived by a lateral fusion of the arms of the proendosternite with the postcoxal bridge. Originally species of *Zolodinini* (Fig. 30) were regarded as the only tenebrionids with externally open procoxal cavities (Watt, 1974), but Doyen and Lawrence (1979) pointed out that they are externally open (internally closed) in *Idisa*. In fact, the externally open condition also occurs in *Platyope* (Platyopini), *Ocnera* (Pimeliinae), *Cryptochile* and *Pachynotelus* (Cryptochilini). In the last two genera the prothorax and mesothorax are adnate, with the ventral articulatory membrane extremely thickened, tough and leathery. In *Pachynotelus* the intercoxal process is expanded laterally, partially closing the cavities. In both genera internal closure, which usually follows external closure, is complete. It seems obvious that the open condition here is secondary, resulting from the close association of the pro- and pterothoraces. In Pimeliini and Platyopini, the prothorax is relatively free, suggesting that open cavities could be the primitive condition. The cavities are internally closed, however, which suggests that the externally open state is again secondary. On the cladograms open cavities appear only as a reversal, even in *Zolodinini*.

Internal closure is more variable. In Erodiini, Stenosini, Cnemeplatiini, Eurychorini and some Asidini the cavities are narrowly open internally, apparently a primitive condition (Fig. 31). In the pimeliine and tentyriine lineages internal closure is effected by close apposition of the posterior edge of the procoxal cowling and the postcoxal bridge along their entire lengths (Fig. 32). In this type of closure (tentyriine closure) usually only a tiny aperture remains near the intercoxal process. The coxal

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←  
 tacoxal region; 37. *Vernayella ephialtes* Koch. ext = external procoxal closure; int = internal closure; c2 = mesocoxa; c3 = metacoxa; cc = coxal cowling; m = metepimeron; mt = metendosternite; p = process of metepimeron; pre = prementum.

cowling and postcoxal bridge are not fused, however, and may easily be separated by gentle pressure. In contrast in the asidine lineage (Fig. 33) the aperture near the intercoxal process is usually much larger and the contact between coxal cowling and postcoxal bridge much shorter, but the cowling and bridge are strongly, usually rigidly, fused. This configuration is termed asidine closure. Intuitively it would seem that these two styles of closure are independently derived from the open condition. In Fig. 209, however, the tentyriine type closure is derived from the asidine type; in Fig. 211 the asidine type is derived twice from the tentyriine type.

**Thoracic fusion (Character 33).** Compressed into this single character is extensive and complex variation. In the primitive state the prothorax is joined to the mesothorax by a flexible membrane, allowing the former to telescope over the constricted anterior margin of the latter. This condition allows torsion as well as dorsoventral and lateral flexibility, although these are relatively limited in many Pimeliinae. In some tribes, such as Pimeliini, Platyopini, and Cryptoglossini the pro- and mesothorax are very closely connected by a somewhat thickened membrane, but significant flexibility remains. In several others the thoracic segments are effectively fused by a variety of autapomorphic mechanisms which are described below. 1. Edrotine type fusion. The proendosternite and mesendosternite are fused as two solid rods between the procoxal and mesocoxal cowlings (Doyen, 1968: fig. 5). Probably this arrangement was evolved via fusion of opposed endosternal muscle discs. Fused pro- and mesendosternal muscle discs occur in *Epiphysa* and are clearly derived from the opposed discs joined by short, thick muscles in other genera of Adesmiini. In *Edrotes* the ventral part of the membrane connecting the pro- and mesosterna is thick and leathery. 2. Erodiiine type fusion. In all genera of Erodiiini the prothorax and mesothorax are very closely adjoined. The endosternites are contiguous but not fused. The ventral articulatory membrane is very short and ligamentous, affording almost no movement. The postcoxal bridges are absent, leaving the procoxal cavities (secondarily?) open. The elytra are mechanically interlocked with the posterior pronotal surface (Fiori, 1977), further rigidifying the prothoracic-mesothoracic joint. 3. Cryptochiline type fusion. The prothorax and mesothorax are solidly fused along their entire ventrolateral and ventral margins. Ventrolaterally the fusion is between the inwardly flanged edges of the hypomerion and the mesothoracic episternum. Ventrally the articulatory membrane has become strongly sclerotized so that the procoxal cowlings appear to be continuous with the mesosternum. The postcoxal bridges are abbreviated or absent. There is essentially no flexibility in this type of joint, which occurs in *Cryptochile*, *Pachynotelus*, *Horatoma*, *Calognathus* and *Vansonium*. 4. Nycteliine type fusion. As in Erodiiini the thoraces are very tightly adjoined, with a very short articulatory membrane which is sclerotized, as in Cryptochilini. As in the latter, the procoxal cowlings appear to be continuous with the mesosternum. Unlike Cryptochilini the hypomera and mesepisterna are not fused. In most genera the postcoxal bridges are complete, so that the pro-mesothoracic joint appears normal externally. In *Nyctelia* and *Psectrascelis* the postcoxal bridge is extremely narrow and laminar, giving the external appearance of open procoxal cavities.

The most likely function of pro-mesothoracic fusion is probably defensive. Most of the taxa which display this modification are ambulatory surface dwellers; Erodiiini and some Edrotini are sand swimmers, while *Pachynoteles* and *Calognathus* dig burrows in sand. This variation in substrate activity indicates that fusion does not



have a locomotory related function. Most of the taxa with the fused pro-mesothoracic joint also have very hard, tough cuticle, again suggesting a passively defensive function. Water conservation might also be important.

**Mesocoxal closure (Character 34).** This character has previously been considered at some length (Doyen and Tschinkel, 1982: 136; see also Doyen, 1987: figs. 4–6). In non-pimeliine lineages the mesocoxal cavities are almost always closed laterally by the mesepimeron which is certainly the primitive condition. Most non-pimeliines with closure effected by the sterna are of small body size, although no functional reason for this correlation is evident. In Pimeliinae closure is usually by the sterna (Figs. 36, 37) and there is no correlation with size. In the cladograms this character is changed to the derived state in the basal stem, then reversed in the asidine lineage (Stem 100) and in several individual OTU's, such as *Ceratanisini* and *Anepsini*. Additional reversals (back to the derived state) occur in *Nycteliini* and *Asidini*, yielding a total of eight changes of state and a consistency index of 0.11. The retention index, however, is 0.66.

**Configuration of mesendosternite (Characters 35–39).** The primitive configuration entails a pair of arms that extend a short distance horizontally or in an oblique anterodorsal direction from the mesocoxal inflexions, then bend laterodorsad toward the mesopleural wing processes. The arm is usually expanded to accommodate muscle insertions near the point of the bend. This topology is closely matched in *Tenebrio* (Doyen and Tschinkel, 1982: fig. 23), and occurs in primitive Pimeliinae such as *Ceratanisus* and *Lixionica*, as well as many *Asidini*, and *Coniontini*. Modifications of the plesiomorphic structure involve (1) Elongation of the horizontal part of the arm, often to the vicinity of the mesothoracic foramen (Char. 38; see Doyen, 1972: fig. 14). (2) Enlargement of the apices of the horizontal arms (Char. 37), as an oblique or horizontal flange, or, in the most apomorphic condition as a large vertical muscle disc (Doyen, 1968: fig. 4). The large ventral muscles which retract the prothorax over the mesothoracic constriction insert on these discs. In a few taxa the apical muscle disc becomes fused with the mesosternal rim (Char. 35). (3) The dorsal part of each arm arises subterminally from the horizontal arm, often near its midpoint (Char. 39). The dorsal arms may also be much abbreviated or absent (Char. 36). Character 35 does not form synapomorphies above the tribal level. None of these characters has a very high consistency index, but the retention indices are mostly moderate.

**Configuration of metendosternite (Characters 40–42).** This structure exhibits extensive variation in form and proportion, most of which is very difficult to codify and polarize because of intermediacy and high levels of obvious homoplasy. Selected variation is illustrated by Doyen and Tschinkel (1982: figs. 25–31). Often metendosternal features are related to general body form. For example, width of the stalk is very strongly correlated to degree of separation of the hind coxae. Only a few, easily polarized characters were included here, including two fusions of the endosternite with the external body wall. Fusion with the mesocoxal inflexions occurs in a few diverse taxa, almost certainly as a homoplasy. Fusion also occurs with various parts of the dorsum (Char. 41). In *Zophosini* the large apical muscle disk is not actually fused to the membranous dorsum, but attached by a short, tendonous muscle. These various states appear to have arisen independently and were coded nonadditively. Relative arm length often is consistent within tribes, but forms few synapomorphies above the tribal level.

**Metacoxal configuration (Characters 43-46).** Primitively the metacoxae are elongate, oriented at nearly right angles to the longitudinal body axis, and almost contiguous medially, as in *Tenebrio*, *Zolodinus*, and most other winged species. Laterally the coxa abuts the metepimeron, which projects posteriorly as a rounded boss which fits into a socket in the laterotergite of the third abdominal segment (first visible segment)(Fig. 34). In many flightless Tenebrionidae, including Pimeliinae, the metacoxae are much less elongate, becoming almost round in tribes such as Adesmiini and Cryptochilini. This change in shape is usually accomplished by a great increase in the distance between the coxae, which in effect have become lateralized in position (Fig. 36a). In several other flightless taxa, however, such as Trientomini, Triorophini and Trimytini, the coxae have retained the primitive condition.

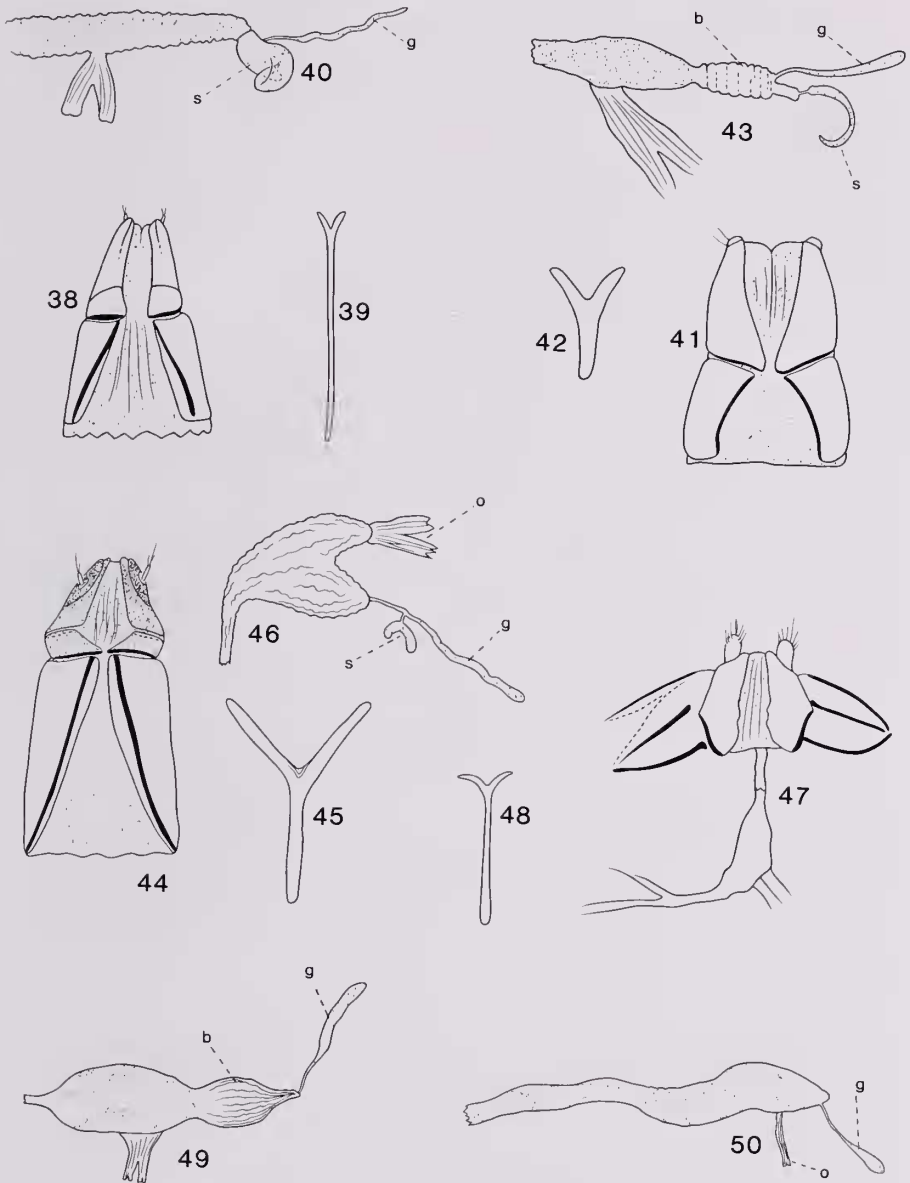
In a few specialized forms the metacoxal cavities are closed by the sterna of the metathorax and third (first visible) abdominal segment (Fig. 35). In these taxa the lateral part of the metacoxa is concealed by the sternites, and the coxal articulation is still with the metepimeron. The less specialized condition occurs in *Alaudes* and *Idisia*, where the metepimeron is not markedly modified (state 1; Fig. 35). In Cryptochilini the metepimeron is produced inward as a prominent boss on which the coxa articulates (state 3; Figs. 36, 36a). Cryptochilini and Cnemeplatiini differ in numerous other characters, and it is almost certain that these states have arisen independently.

In Caenocrypticini lateral coxal closure is between the metepimeron and abdominal sternite, but the metepimeron is broad, affording a much more rigid joint (Fig. 37).

**Ovipositor configuration (Characters 47-64).** The ovipositor is extremely variable in Tenebrionidae, ranging from a large, strongly sclerotized, blade-like organ (e.g., *Talanus*, *Hegemona*, *Saziches*, *Acropteron*) to an atrophied, membranous remnant (*Rhipidandrus*, Phrenapatini)(Tschinkel and Doyen, 1980). In the most primitive ovipositors the coxites are divided into four lobes, the apical being long and digitate and terminally bearing long, slender gonostyles. In more derived forms the apical lobe is incorporated into the ovipositor shaft, usually becoming shorter and more or less adnate to the preapical lobe. Fusions may occur, so that the number of lobes is two or three, and the reduced gonostyles usually attach laterally on the apical coxite lobe. Additional changes in the orientation of the basal coxite lobe or in the proportions of the coxites and paraprocts have resulted in dramatically apomorphic ovipositor configurations, as in the tribe Coelometopini, for example.

No Pimeliinae have the primitive type of ovipositor described above, and none show the major structural modifications of the type illustrated by Coelometopini or Talanini. Even so the range of variation is impressive, and, as in non-pimeliine lineages, the ovipositor appears generally to offer more information for classification at higher levels than do the male genitalia, which are more useful at the generic level and below.

The least derived pimeliine ovipositor appears to be that of *Boromorphus* (Fig. 72), where four short unsclerotized coxite lobes are present and the gonostyli are apical and moderately large. *Alaephus* (Fig. 148), *Ceratanisus* (Fig. 78) and Akidini (Figs. 83, 84) have relatively large gonostyli, but they are subapical and the coxite lobes are reduced to three with the apical one sclerotized. In most other groups of Pimeliinae gonostyli are lateral and greatly reduced, coxite lobing is more or less obliterated by fusion and sclerotization, and the apical lobe is often produced as a



Figs. 38–50. Female genitalia of Stenosini and Cnemeplatiini. 38–40. Ovipositor (ventral), spiculum and internal tract (lateral) of *Grammicus chilensis* Waterhouse; 41–43. Same, *Araeoschizus sulcicollis* LeConte; 44–46. Same, *Stenosis sardoa* Küster; 47, 48. Ovipositor and spiculum of *Typhlusechus ignotus* Doyen; 49. Internal tract of *Lepidocnemeplatia sericea*; 50. Same, *Alaudes singularis*. b = bursa copulatrix; g = spermathecal accessory gland; s = spermatheca.

sclerotized digging prong, sometimes of diagnostic shape. Pimeliini, Asidini and genera such as *Cnemodinus*, *Trilobocara* and *Salax* are good examples (Figs. 152, 154, 162). The usual variation in coxite: paraproct proportions is present, and several taxa have the ovipositor reduced, sometimes extremely so (e.g., *Typhlusechus* (Fig. 47), *Cnemeplatiini*, *Falsomycterus*).

Since the female reproductive system has barely been investigated for Pimeliinae and because of the difficulty in adequately describing it, both the ovipositors and internal female tracts are extensively illustrated. These illustrations are ordered systematically, according to the arrangement in Appendix III. Variation in the salient features of pimeliine ovipositors is briefly characterized below.

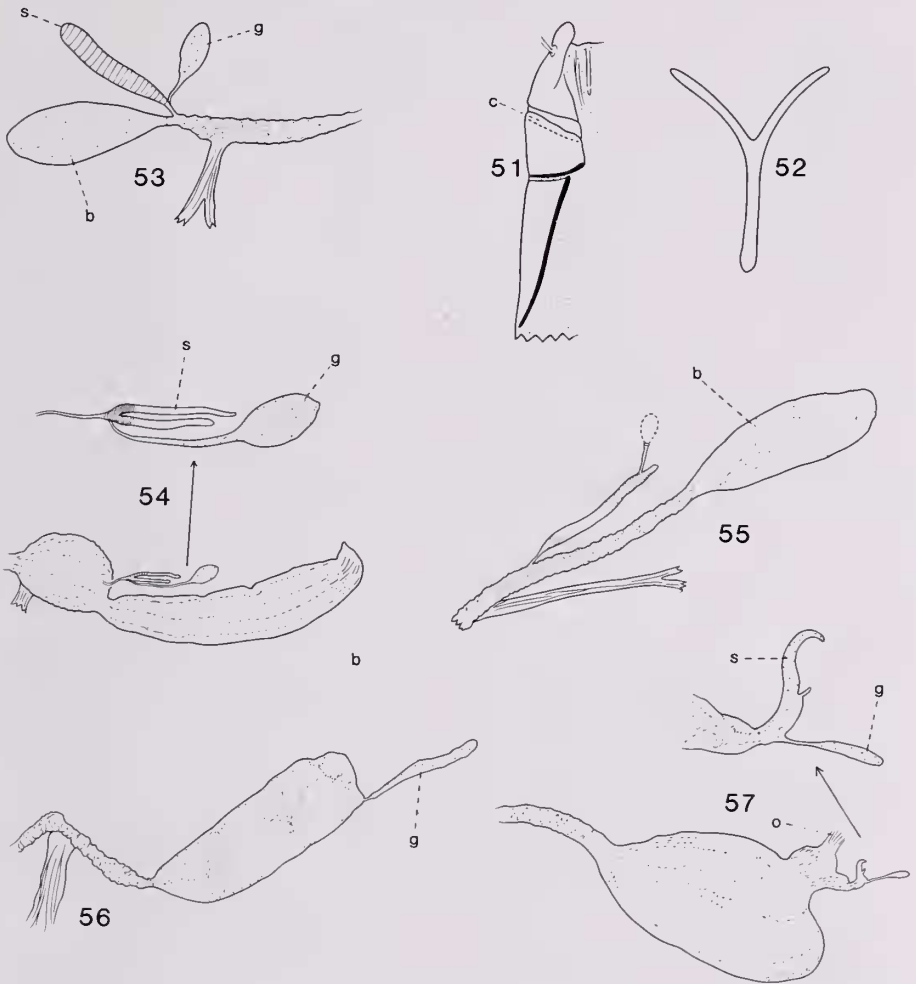
Ovipositor size (Chars. 47, 60). Character 47 differentiates taxa in which the ovipositor is rudimentary. Coxites and proctigers are reduced, often unrecognizable, and the spiculum is rudimentary or absent, indicating that these ovipositors are not extruded and retracted. In other taxa the ovipositor ranges from very short but completely formed (e.g., *Araeoschizus*, Fig. 41) to very elongate (e.g., Asidini), as reflected by character 60. Derived states of both these characters are scattered on the cladogram, with low consistency but moderate retention indices.

Proportions of coxite, proctiger and spiculum (Chars. 48, 55, 59). In nearly all taxa the proctiger and its ventral baculus are about the same length (as in Figs. 38, 66, 87). In *Vernayella* (Caenocrypticini) and in a few genera of other tribes the baculus is much shorter than the dorsal part of the proctiger (Figs. 75, 84). Similarly, the spiculum, to which the ovipositor protractor and retractor muscles attach, is almost always subequal in length to the ovipositor shaft (not including the basal telescoping membrane). Relatively short but functional spicula occur primarily in taxa with long ovipositors, such as Asidini and Pimeliini (shortening occurs non-synapomorphously in taxa with rudimentary ovipositors, such as *Cnemeplatiini*). Conversely, long spicula occur mostly in taxa with short ovipositors (e.g., Edrotini, Fig. 186). Relative lengths of coxite and paraproct (Char. 59) vary by about a factor of three. Variation in ovipositor length is generally the result of change in paraproct length, so that taxa with long ovipositors (e.g., Asidini, Branchini; Figs. 137, 142) have long paraprocts, those with short ovipositors (Stenosini, Caenocrypticini, Anepsiini; Figs. 38, 41, 75, 114) have short paraprocts. Ovipositor proportions are extremely variable in non-Pimeliinae. Intermediate character states, which occur in the majority of taxa, were selected as hypothetically primitive.

Gonostyle size and position (Chars. 49, 50) are discussed above.

Coxite configuration (Chars. 51-54, 56, 64). In many non-pimeliine tenebrionids such as *Tenebrio* (Doyen, 1966: fig. 72), four distinct coxite lobes are apparent. In Pimeliinae four lobes seem to be present in *Boromorphus* and *Eupsophulus* (Figs. 72, 146) but the lobing is indistinct. Three evident lobes are present in a number of taxa such as *Lasostola*, *Nyctoporis* and *Megelenophorus* (Figs. 96, 120, 126), but in the great majority lobing is obscured by overall sclerotization of the coxites, especially apically. In most members of the large asidine and tentyriine-eurytmetopine lineages the three apical lobes are largely consolidated with only faint divisions if any (Figs. 137, 144, 189, 193). The basal lobes, however, are almost always separated from the apical part of the coxite by a transverse pleat in the membrane which forms a shallow pocket opening posterad (Char. 53, Figs. 63, 78, 133, etc.) marking a point of dorsoventral flexibility in the ovipositor shaft. The function of this cleft is not known.

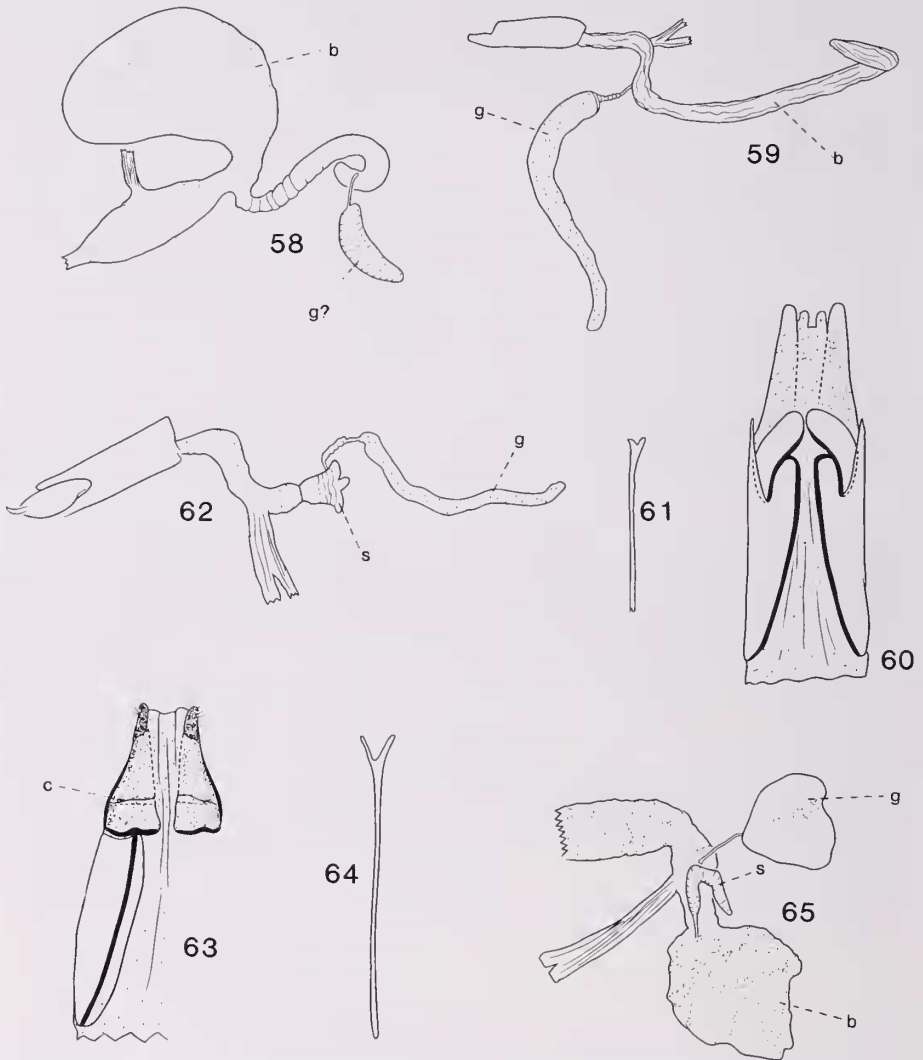




Figs. 51–57. Female genitalia of Eurychorini and Erodiini. 51–53. Ovipositor, spiculum and internal tract of *Adelostoma grande* Haag. 54. Internal tract of *Lepidochora eberlanzi* Gebien; 55. Same, *Eurychora barbata*; 56. Same, *Apentanodes globosus* Reiche; 57. Same, *Erodius carinatus* Solier. b = bursa copulatrix, c = cleft in coxite; g = accessory gland; s = spermatheca(e).

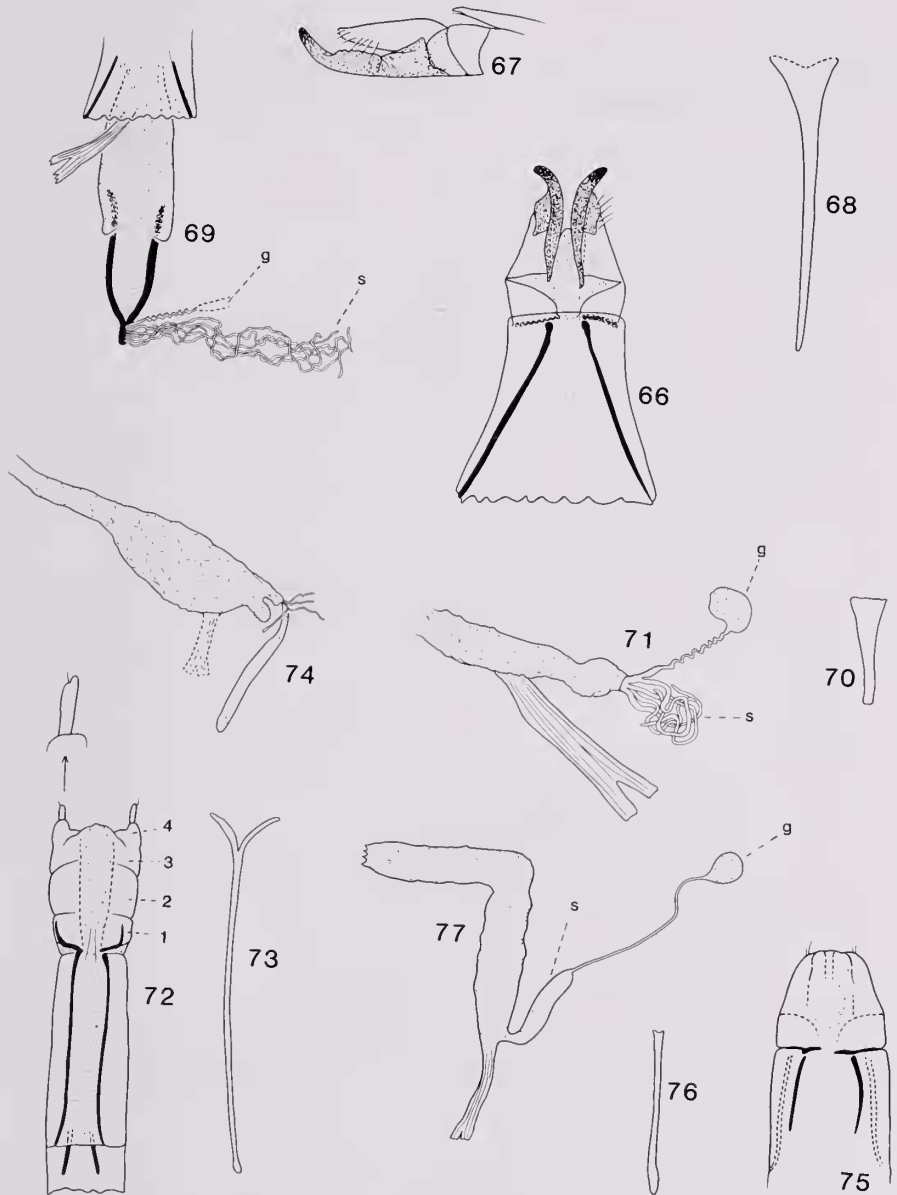
It could be important during insertion of the ovipositor into soil or in facilitating movement of the eggs, which are notably large in many Pimeliinae. On the cladograms this character has low consistency but high retention, characterizing most of the members of the combined pimeliine, asidine and tentyriine-eurymetopine lineages (stem 14). In stem 31 (Coniontini, Branchini, Asidini), in which the entire coxite becomes sclerotized, the transverse cleft is lost.

One of the most striking features of the pimeliine ovipositor is the elaboration of the fourth coxite lobes into strongly sclerotized digging structures (Chars. 54, 64).

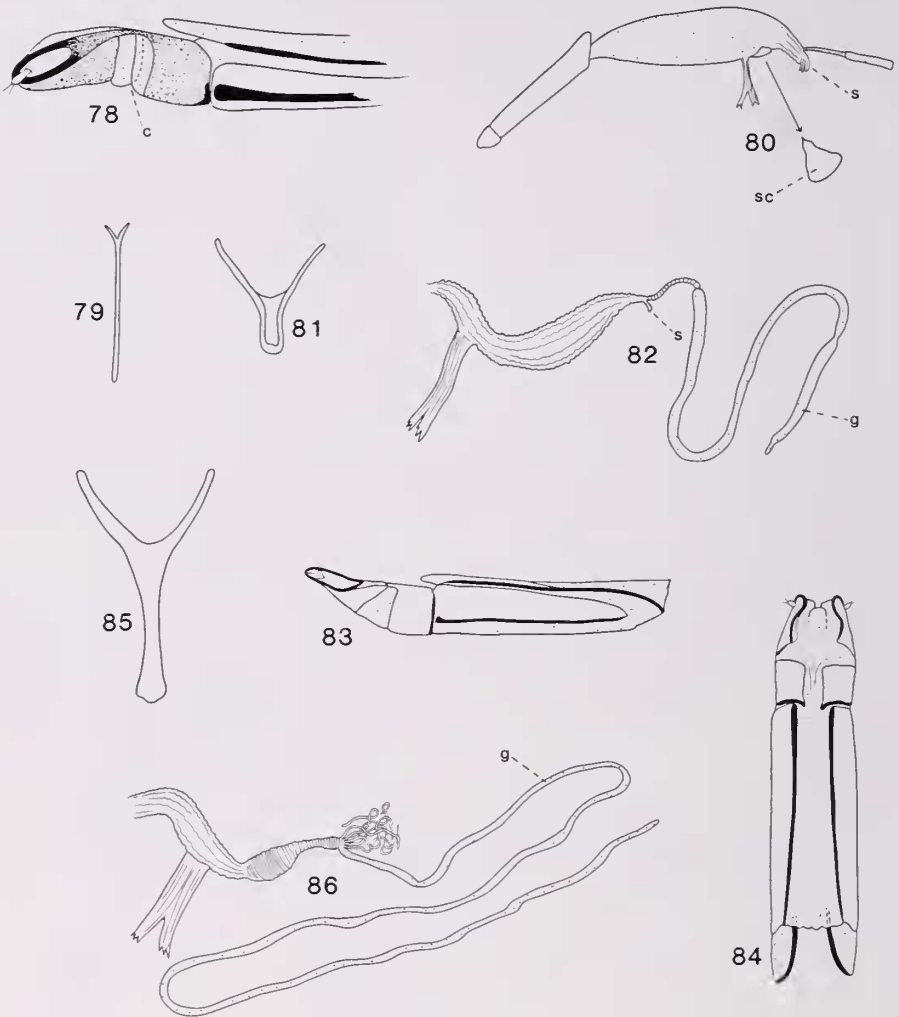


Figs. 58-65. Female genitalia of Zophosini. 58. Internal tract of *Zophosis* (*Gyrosis*) *orbicularis*; 59. Same, *Z. (Z.) testudinaria*; 60-62. Ovipositor, spiculum and internal tract of *Z. (Cerosis) herreroensis* Gebien; 63-65. Ovipositor, spiculum and internal tract of *Z. (Calosis) amabilis* Deyrolle. b = bursa copulatrix, c = cleft in coxite; g = accessory gland; s = spermatheca(c).

Commonly the coxites remain as evenly attenuate lobes when they become sclerotized, but distinctive configurations characterize tribes such as Akidini (Figs. 83, 84), Pimeliini (Figs. 96, 97) and Cryptochilini (Figs. 87, 92). No obvious morphoclines connect these various forms, and the states of character 64 were considered non-additive.



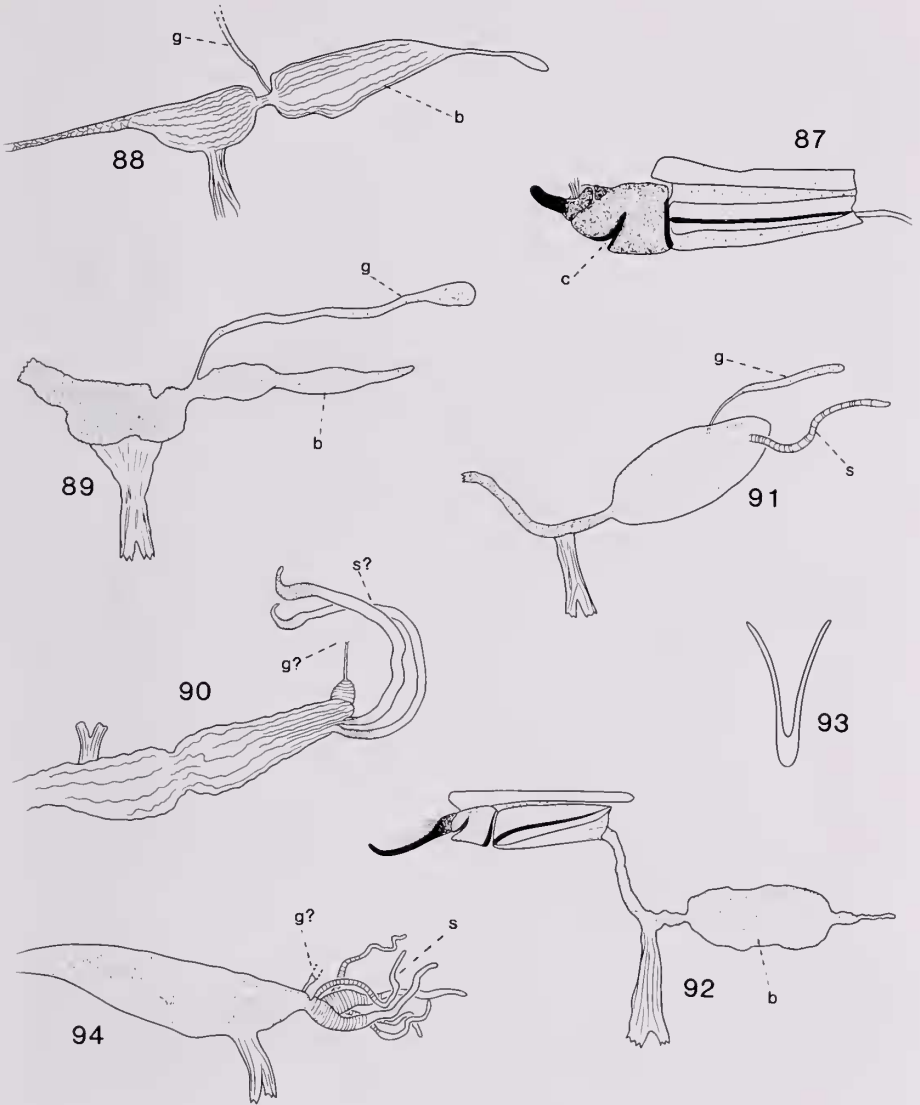
Figs. 66-77. Female genitalia of Boromorhini, Caenocrypticini and Falsomycterini. 66, 67. *Pteroctenus* species (Nova Teutonia, Brazil), ovipositor, ventral and coxite, lateral; 68, 69. Same, spiculum and internal tract; 70, 71. Spiculum and female tract of *Falsomycterus* sp. (Nova Teutonia, Sta. Catarina, Brazil); 72-74. Ovipositor, spiculum and internal tract of *Boromorplus tagenoides* Lucas; 75-77. Ovipositor, spiculum and internal tract of *Vernayella ephialtes*. g = accessory gland; s = spermatheca(e); sc = vaginal sclerite; 1, 2, 3 & 4 = coxite lobes.



Figs. 78–86. Female genitalia of Ceratanisini and Akidini. 78–80. Ovipositor, spiculum and internal tract of *Ceratanisus tristis* Faldeman; 81, 82. Spiculum and internal tract of *Morica planata* Fabricius; 83–86. Ovipositor (lateral and ventral), spiculum and internal tract of *Akis tingitana* Lucas. c = cleft in coxite; g = accessory gland; s = spermathecae; sc = vaginal sclerite.

The base of coxite lobe 1 is strengthened by a transverse baculus which pivots against the ventral paraproct baculus. The shape of this baculus is so variable that it was not possible to recognize meaningful character states. In Molurini, however, the baculus has a strongly oblique orientation, which was considered a derived feature (Char. 56, Fig. 104).

The paraprocts (Chars. 57, 58, 61) are of simple structure. Character states commonly present in non-Pimeliinae were used for polarizing.



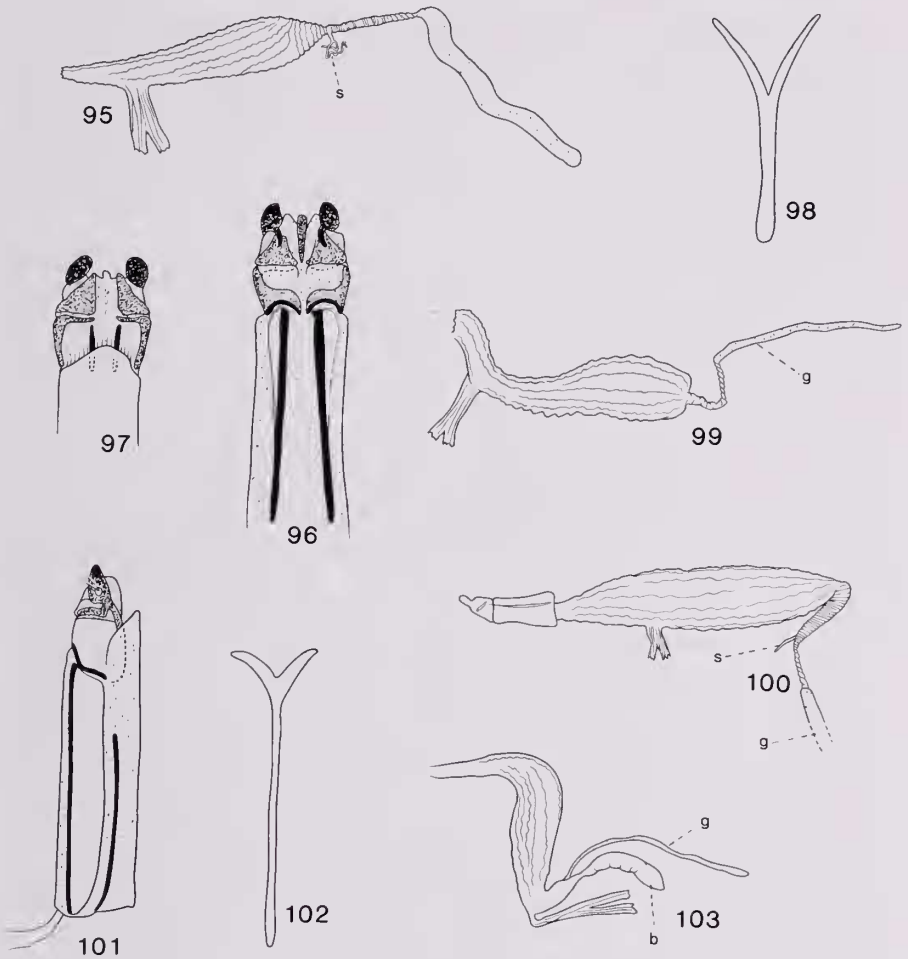
Figs. 87–94. Female genitalia of Cryptochilini and Calognathini 87–88. Ovipositor (lateral) and internal tract of *Cryptochile grossa* Erichson; 89–90. Internal tracts of *Cryptochile* species (Spektakalpas, Cape Province, South Africa) and *Horatoma parvula* Solier; 91. Internal tract of *Pachynotelus dimorphus* Koch; 92–93. Ovipositor and internal tract (lateral) and spiculum of *Pachynotelus albonotatus*; 94. Internal tract of *Calognathus chevrolati* Guérin. b = bursa copulatrix; c = cleft in coxite; g = accessory gland; s = spermatheca(e).



Spiculum configuration (Chars. 62, 63). The reflexed spicular arms of Molurini (Fig. 105) are certainly derived and almost autapomorphic (similar in a few Eurychorini and Vacronini). The primitive state of character 62, however, is problematic. States 2 (Figs. 45, 52, 118) and 3 (Figs. 39, 48, 121, 163), common outside Pimeliinae, occur in otherwise primitive taxa such as *Tenebrio* and *Zolodinus*, respectively. State 3 also occurs in Lagriinae, and is here treated as plesiomorphic. State 1, with the arms separate to the base (Fig. 93), could also be primitive, since the spiculum must have arisen from a structure that originally was paired. However, the paired condition is unknown outside Pimeliinae, and within Pimeliinae occurs only in Cryptochilini and Pimeliini, which are relatively apomorphic in most features. The functional significance of these different spicular forms is obscure.

**Internal female reproductive tract (Characters 65-76).** Tschinkel and Doyen (1980) considered the primitive form of the internal reproductive tract to be that of *Lagria*. In this configuration the vagina ends in a sac-like bursa copulatrix which bears dorsally (i.e., opposite the oviduct) a spermathecal gland, without a separate spermatheca. This arrangement occurs in several tribes of Lagriinae, in Phrenapatinae and in a few other non-Pimeliinae (see Tschinkel and Doyen, 1980; Appendix IV). In Pimeliinae comparable internal tracts occur in some Zophosini and Cryptochilini (Figs. 59, 88, 89), and tracts with apical gland and no spermatheca occur in Cnemeplatiini, Pimeliini, and *Thinobatis* (Figs. 49, 50, 99, 175). However, in all the tribes listed above, some genera have more derived configurations, with the Zophosini and Cryptochilini being particularly variable. In Erodiini and many Tentyriini and Adesmiini the primitive form is essentially retained, but the bursa copulatrix has become reduced in diameter and annulate (Figs. 57, 195, 198), forming a more or less definitive spermatheca. A vaguely similar, pouch-like spermatheca occurs at the base of the gland in *Evaniosomus*, *Melaphorus* and *Areyennis* (Figs. 160, 161). In many genera of Tentyriini and Adesmiini the spermatheca has become further differentiated by division into two or three chambers (Figs. 196, 197, 201) and in genera such as *Epitrichia* (Fig. 204) and *Derosphaerius* (Fig. 194) the gland empties into the spermatheca, rather than the vagina. Zophosini are exceptionally variable and not diagnostic at the tribal level. In *Z. (Zophosis) testudinata* (Fig. 59) the tract is as in *Lagria*. In *Z. (Zophosis) orbicularis* the gland empties into a narrow diverticulum of the bursa (Fig. 58), and in *Z. (Cerosis) hereroensis* the gland empties into a capsular spermatheca of peculiar shape (Fig. 62). This structural arrangement is similar to that of *Grammicus* (Fig. 40), but the latter could equally have arisen by specialization of the type of structure exemplified by Tentyriini. The arrangement in *Z. orbicularis* (Fig. 58) is suggestive of that in some Tentyriini, where a reduced, annulate bursa functions as spermatheca (e.g., Fig. 198). In Tentyriini, however, a large, saccate primary bursa is never retained. Finally, in *Z. (Calosis) amabilis*, two diverticula empty into the vagina by independent ducts, while a large bursa is retained (Fig. 65). Pimeliini (Figs. 95, 99, 100), and Cryptochilini (Figs. 88-94) are also variable in the degree of differentiation of the spermatheca, and the number of spermathecal tubes varies as well. I have dissected relatively few genera of these groups, and it may be expected that some of the inferences which follow will require reconsideration.

Most Pimeliinae have both a spermathecal gland and one or more spermathecae. In Stenosini (Figs. 40, 43, 46) and Eurychorini (Figs. 53-55) the spermatheca is a single locular capsule emptying into a common duct with the spermathecal gland.



Figs. 95–103. Female genitalia of Pimeliini and Sepidiini. 95. Internal tract of *Sternoplax zichyi* Csiki; 96, 97. Ovipositor, ventral and dorsal, of *Lasostola ashkabadensis* Bogdanovich and Kaszab; 98, 99. Spiculum and internal tract of same; 100. Internal tract of *Ocnera hispida* Latreille; 101–103. Ovipositor (lateral), spiculum and internal tract of *Sepidium perforatum* Allard. b = bursa copulatrix; g = accessory gland; s = spermatheca.

Caenocrypticini appear to have a similar system (Fig. 77), but additional species need to be examined. This arrangement could have been derived from the lagriine type via intermediates such as *Grammicus* (Fig. 40), which is basically similar to some Tentyriini, except that a definite constriction separates the spermatheca from the vagina.

Ceratanisini (Fig. 80) and some Pimeliini, Akidini and Cryptochilini have multiple spermathecae, as mentioned above. In these groups, as in Lagriinae, the spermathecal tube(s) are usually thick and do not join the vagina by a differentiated duct. The

exception is *Akis*, where the tubes arise laterally from the spermathecal gland duct (Fig. 86). This is basically similar to the arrangement in most Pimeliinae, where one to (usually) many spermathecal tubes empty into the common duct which also bears the spermathecal gland. The spermathecae may be arranged apically on a common duct, as in Asidini, Coniintini, etc. (Figs. 125, 128, 132, 134–145) or they may arise independently from the side of the gland duct, as in Eurymetopini and many others (Figs. 147, 150–152, 165, 172, 178–180). These major configurational differences are described by Characters 65, 67, 68 and 76.

The remaining reproductive tract characters describe more superficial differences, and are mostly self explanatory. The spermathecal duct (Char. 69) is undefined in *Akis* and *Asida* (Figs. 86, 143) but well developed in many other Asidini (Figs. 140, 142). The common duct receiving both the spermathecae and the gland (Char. 70) is usually unpigmented and flexible. In Epitragini it is brownish, thick walled, annulate and more or less rigid (Figs. 165, 168–171). This is an autapomorphy for Epitragini.

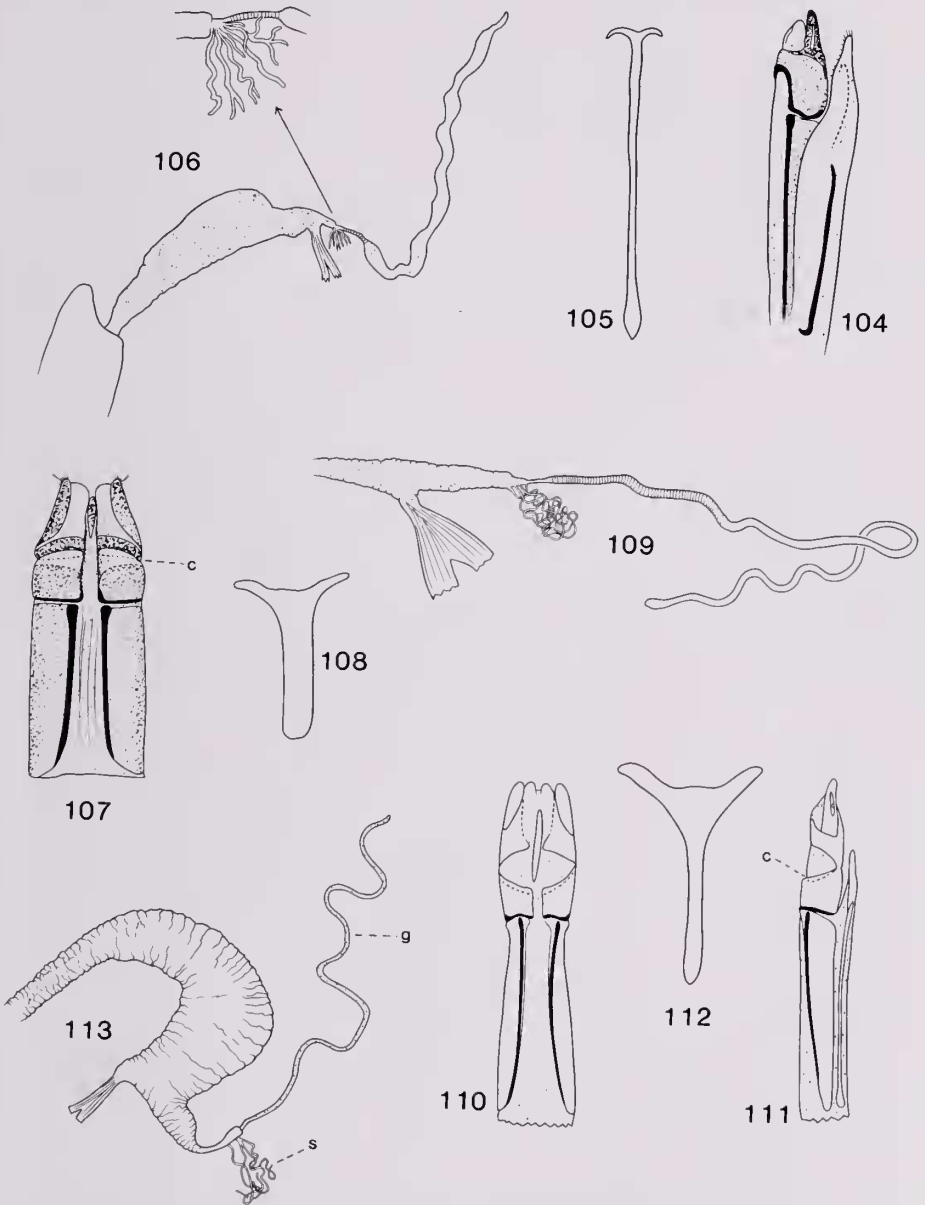
A secondary bursa copulatrix is seldom present in Pimeliinae. It may be recognized by the insertion of both oviduct and spermatheca/gland duct on the same side of the vagina, as in *Salax*, *Edrotes* (Figs. 164, 187) and a few other genera.

**Abdominal venter and elytra (Characters 77, 79, 80).** The internalization of the articular membranes between sternites five to seven has been discussed at length (Doyen, 1972; Watt, 1974; Fiori, 1977; Doyen and Tschinkel, 1982). It need be mentioned here only that among Pimeliinae the tribes Pimeliini and Platypini are unique in having exposed membranes, possibly a secondarily evolved specialization.

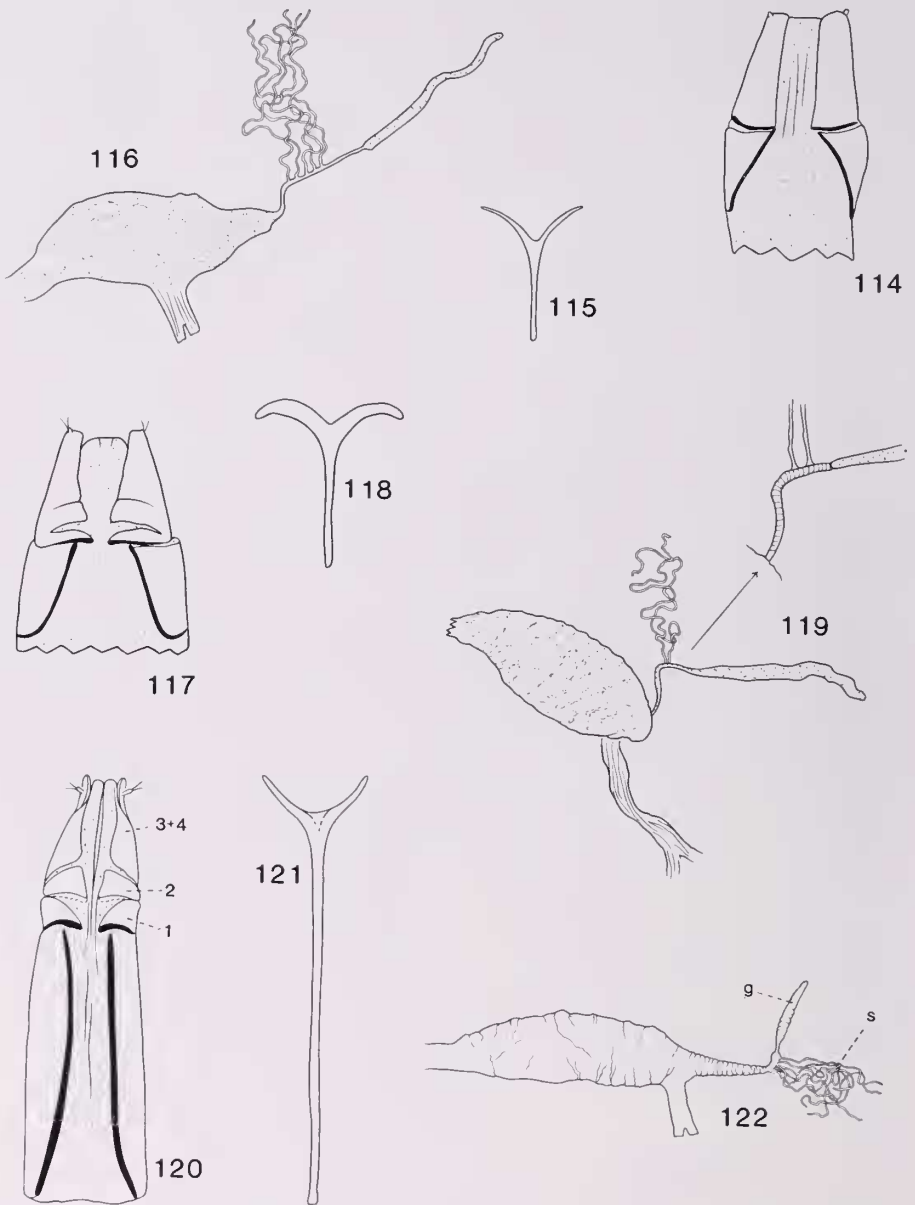
The joints between the elytra and the abdominal sternites were investigated in several pimeliine genera by Fiori (1977), who examined the joints between elytra and thoracic epimera and at the elytral midline, as well. The most generalized condition occurs in winged taxa, where an epipleural ridge on the elytron fits loosely into a groove on the sternum at rest. In nearly all other Pimeliinae the elytra and sternites are immovably coapted, as are the two elytra along the midline. Fiori (1977) recognized two different mechanisms of coaptation between elytra along the medial suture. One mechanism, involving a single dovetail, was observed in *Akis* and *Asida*. A different mechanism, involving double dovetails, was described in *Pimelia* and *Mesostena*. After comparing a much larger number of genera, I believe that elytral interlocking mechanisms cannot be simply divided into these two types. *Platyope*, for example, closely related to *Pimelia* has an interlocking structure which appears intermediate between the two types. *Pachychila*, close to *Mesostena*, has a single dovetail mechanism. *Heterasida*, a typical member of Asidini by other features, has a complex mechanism with two dovetails. In addition there is significant variation in details of the male and female parts of the structures.

Fiori recognized three categories of junction between elytra and abdominal sternites. Simple coaptation without interlocking was observed in winged and some wingless genera (Fig. 205); a single dovetail mechanism was observed in most wingless forms; and a double dovetail mechanism in *Blaps*. In my broader survey of Pimeliinae I recognized two types of single dovetail interlocking, differing in the degree of constriction of the male element (Figs. 206, 207), as well as a third, amplexiform type in Molurini in which the elytral epipleuron has a very broad overlap with the expanded laterotergite without any interlocking (Fig. 208).

In general it seems obvious that elytral interlocking mechanisms have evolved

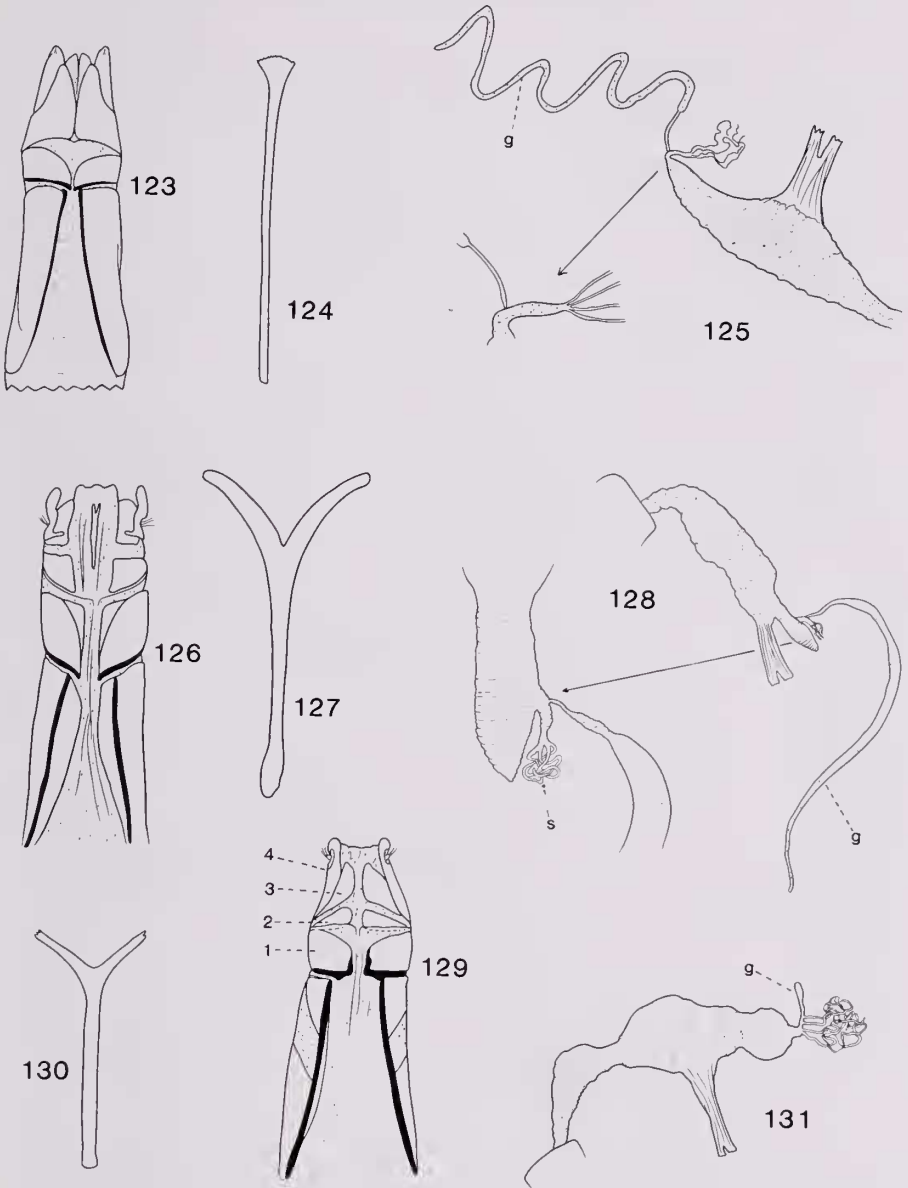


Figs. 104–113. Female genitalia of Molurini and Cryptoglossini. 104–106. Ovipositor (lateral), spiculum and internal tract of *Phrynocolus dentatus* Solier; 107–109. Ovipositor, spiculum and internal tract of *Cryptoglossa laevis* LeConte; 110–113. Ovipositor (ventral and lateral), spiculum and internal tract of *Centrioptera asperata* (Horn). c = cleft in coxite; g = accessory gland; s = spermathecae.

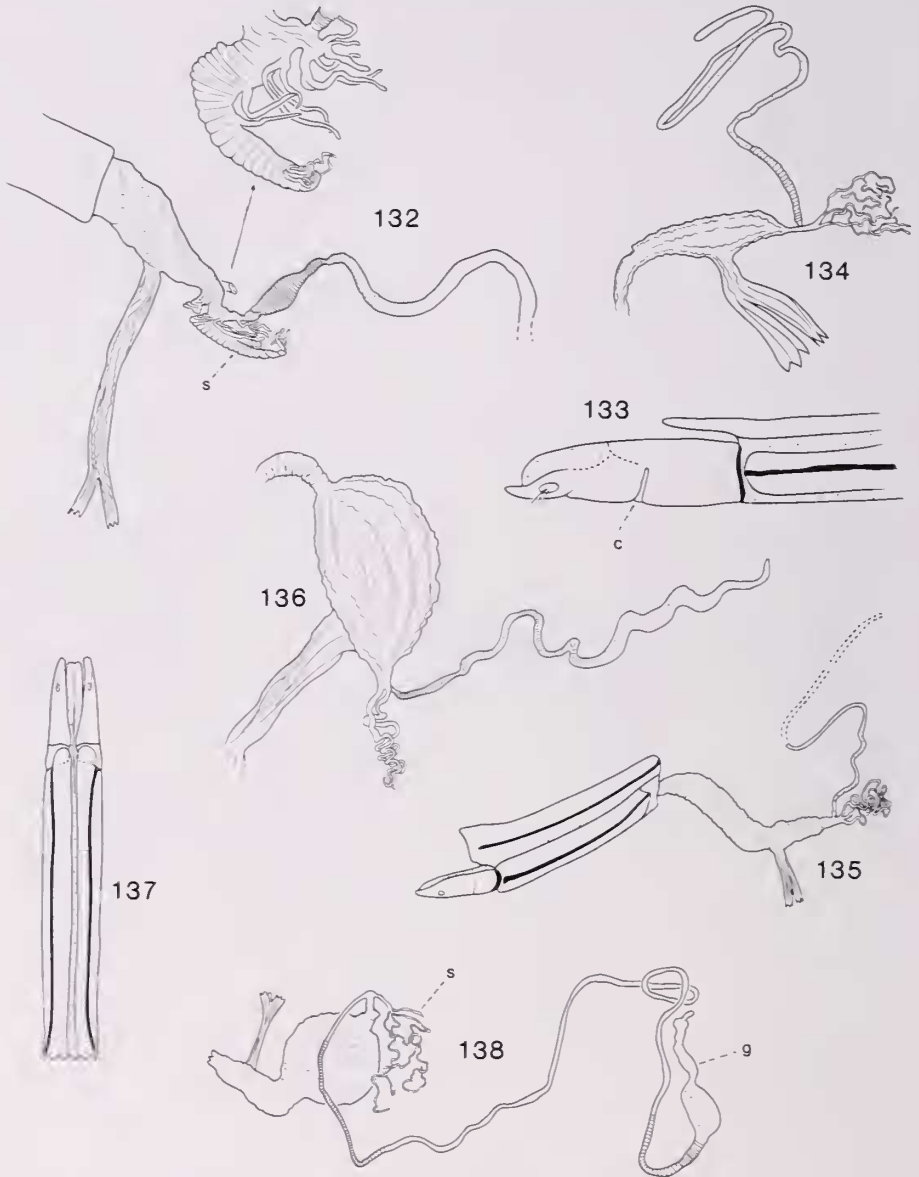


Figs. 114–122. Female genitalia of Anepsini and Nyctoporini. 114–116. Ovipositor, spiculum and internal tract of *Anepsius delicatulus* LeConte. 117–119. Same structures, *Anchomma costatum* LeConte; 120–122. Same structures, *Nyctoporis carinata* LeConte. c = cleft in coxite; g = accessory gland; s = spermatheca; 1, 2, 3 & 4 = lobes of coxite.

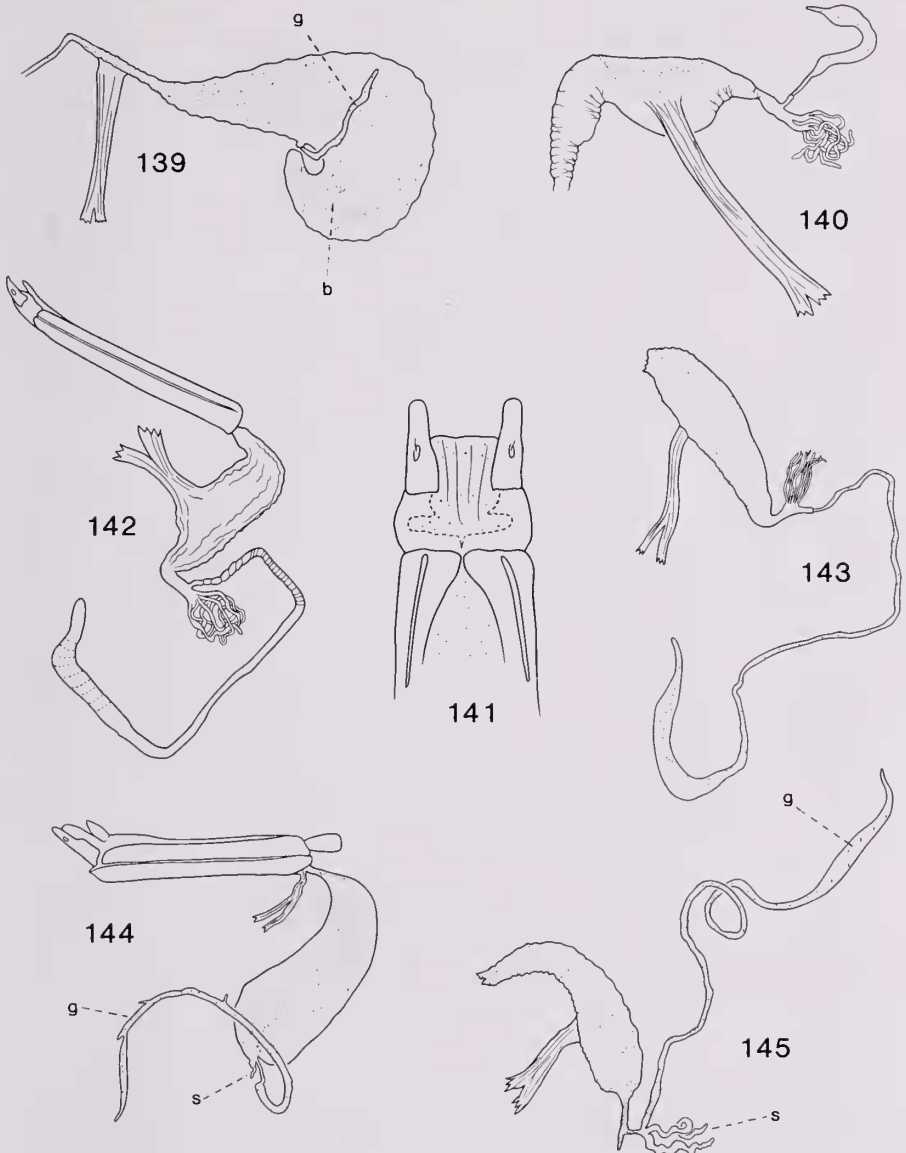




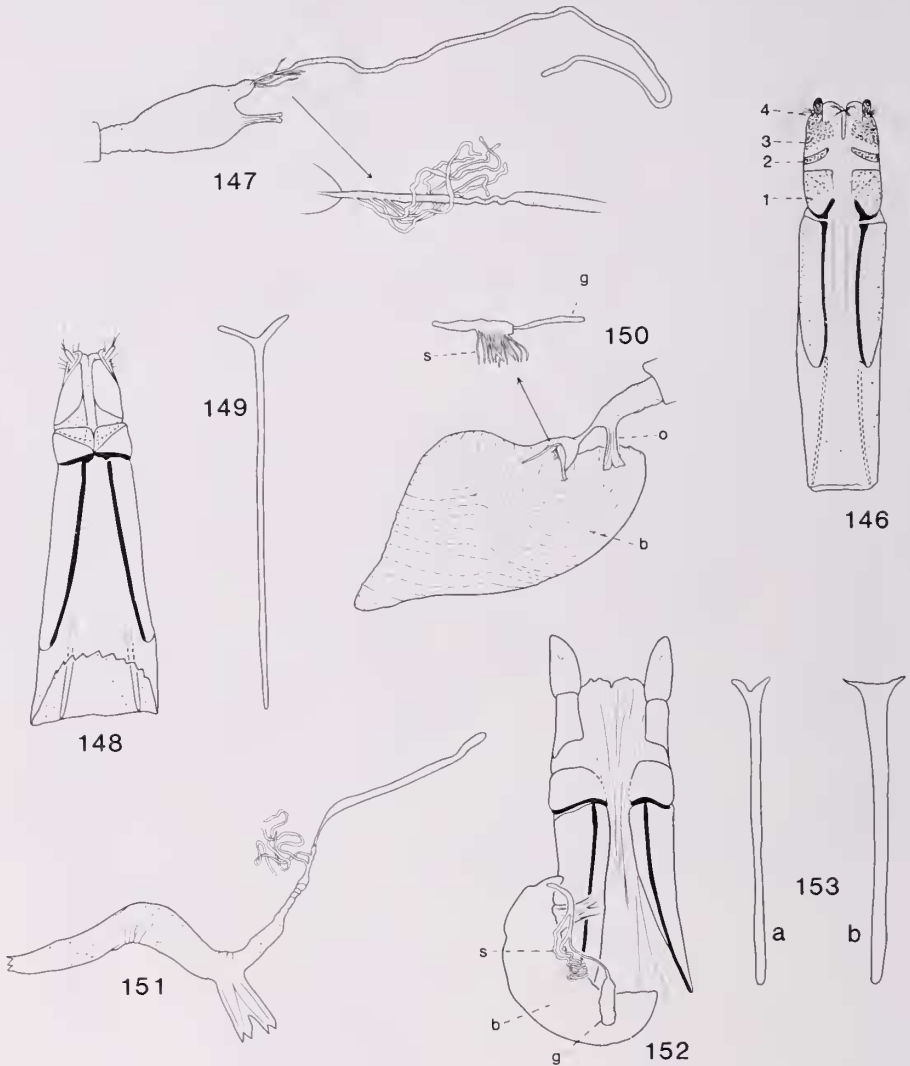
Figs. 123–131. Female genitalia of Elenophorini. 123–125. Ovipositor, spiculum and internal tract of *Elenophorus collaris* Linnaeus; 126–128. Same, *Megelenophorus americanus* Lacordaire; 129–131. Same, *Psammetichus pilipes* Guérin. g = accessory gland; s = spermatheca(e); 1, 2, 3 & 4 = lobes of coxite.



Figs. 132–138. Female genitalia of Nyctelini, Praocini, Physogasterini and Branchini. 132. Internal tract of *Gyriosomus paulseni* Fairmaire; 133, 134. Ovipositor (lateral) and internal tract of *Platestes depressus* Guérin; 135. Ovipositor and internal tract of *Physogaster penai* Kulzer; 136. Internal tract of *Branchus obscurus* Horn; 137, 138. Ovipositor (ventral) and internal tract of *Anectus sordidus* Champion. g = accessory gland; s = spermathecae.

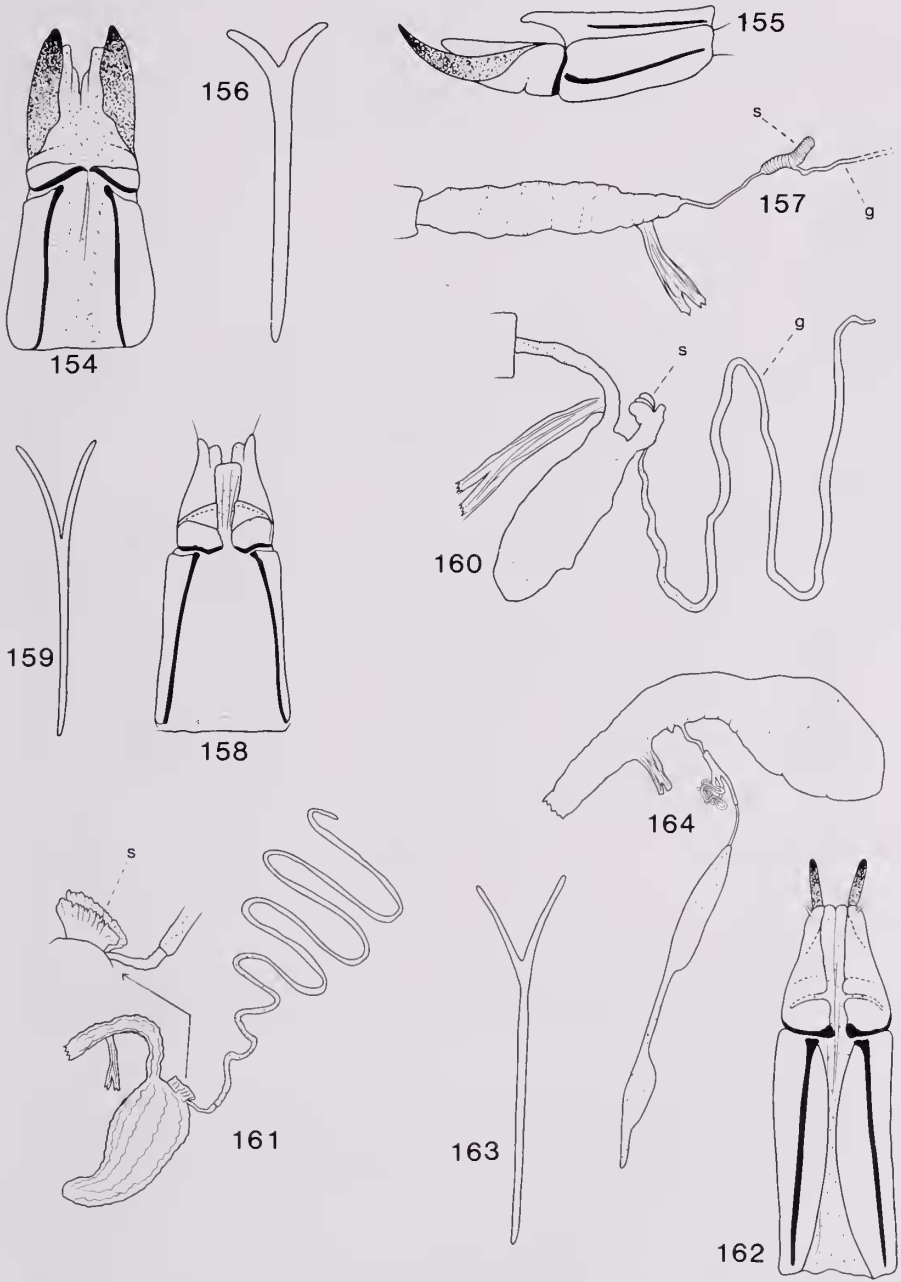


Figs. 139–145. Female genitalia of Asidini. 139, 140. Internal tracts of *Scotinus* sp. (ex. San Francisco, Sta. Catarina, Brazil) and *Ucalegon pulchella* Champion; 141, 142. Ovipositor (ventral) and internal tract of *Craniotus pubescens* LeConte; 143. Internal tract of *Asida allaudi* Escalera; 144. Ovipositor (lateral) and internal tract of *Cardigenius laticollis* Solier; 145. Internal tract of *Pseudomachla* sp. (ex. Botswana, 35 km S Kang). g = accessory gland; s = spermatheca.



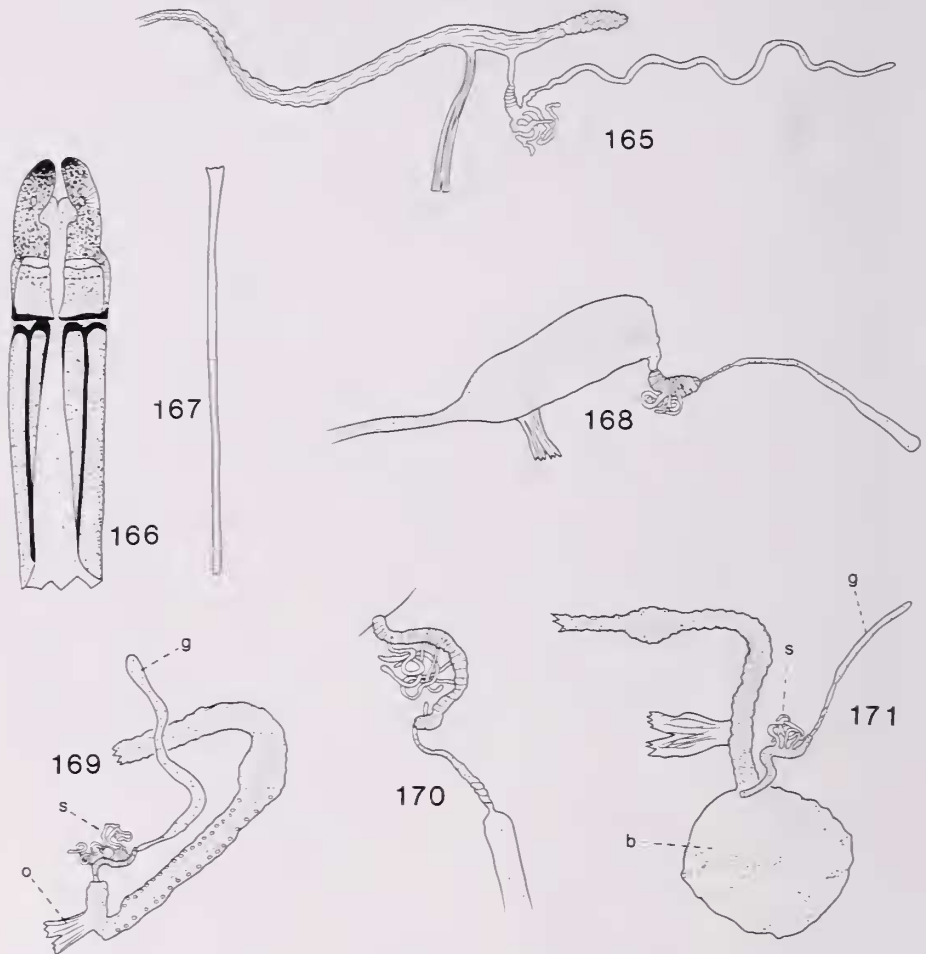
Figs. 146–153. Female genitalia of Vacronini and Cnemodini. 146, 147. Ovipositor and internal tract of *Eupsophulus castaneus*; 148–150. Ovipositor, spiculum and internal tract of *Alaephus pallidus*; 151. Internal tract of *Lixionica angustata* Blackburn; 152–153. Ovipositor plus female tract and spicula from 2 individuals of *Cnemodinus testaceus* Horn. b = bursa copulatrix; g = accessory gland; o = oviduct; s = spermatheca; 1, 2, 3 & 4 = lobes of coxite.

Figs. 154–164. Female genitalia of Trilobocarini and Evaniosomini. 154–157. Ovipositor (ventral and lateral), spiculum and internal tract of *Trilobocara ciliatum* Solier; 158–160. Ovi-



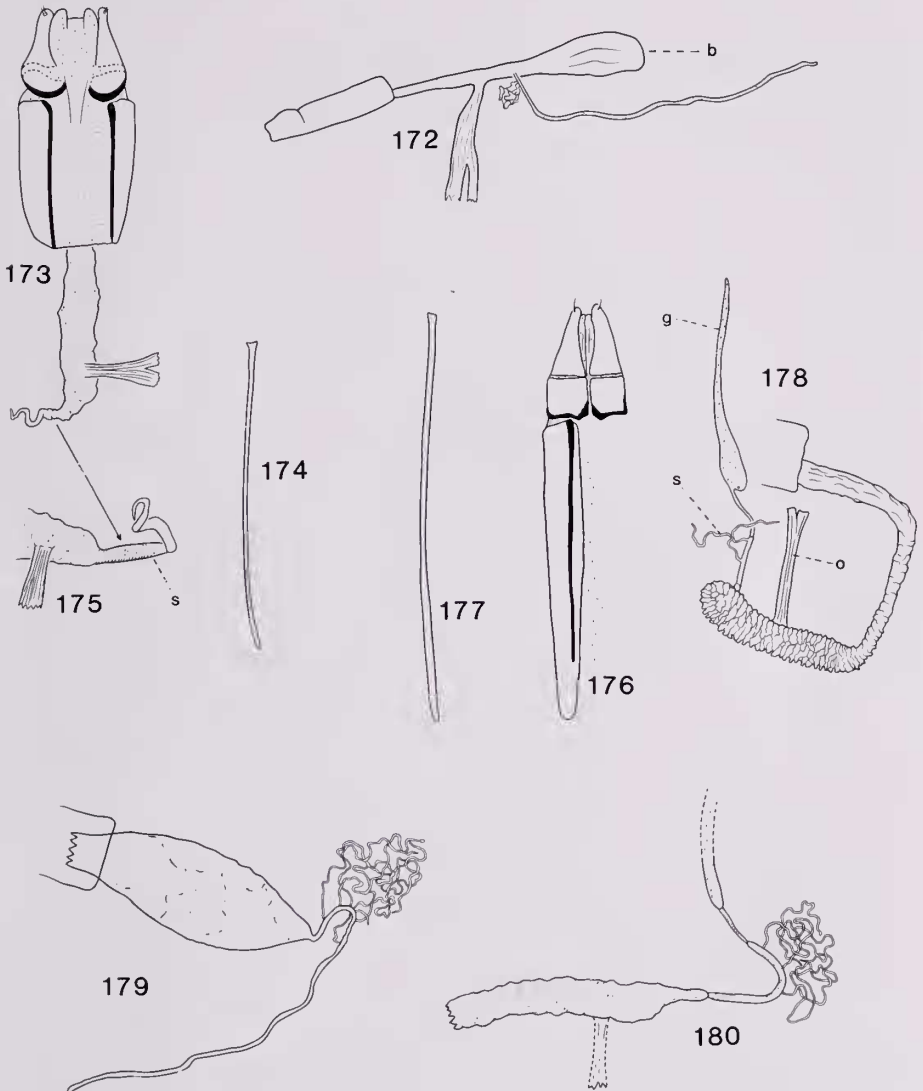
positor (ventral), spiculum and internal tract of *Melaphorus reichei* Guérin; 161. Internal tract of *Aryenis unicolor* Blanchard; 162–164. Ovipositor, spiculum and internal tract of *Salax lacordairei* Guérin. g = accessory gland; s = spermatheca.





Figs. 165-171. Female genitalia of Epitragini. 165. Internal tract of *Epitragus aurulentis* Kirsch; 166-168. Ovipositor, spiculum and internal tract of *Pseudothinobatis grandis* Kulzer; 169-171. Internal tracts of *Hypselops oblonga* Solier, *Nyctopetus rengoensis* Freude and *Lobometopon fusiforme* Casey. g = accessory gland; s = spermatheca.

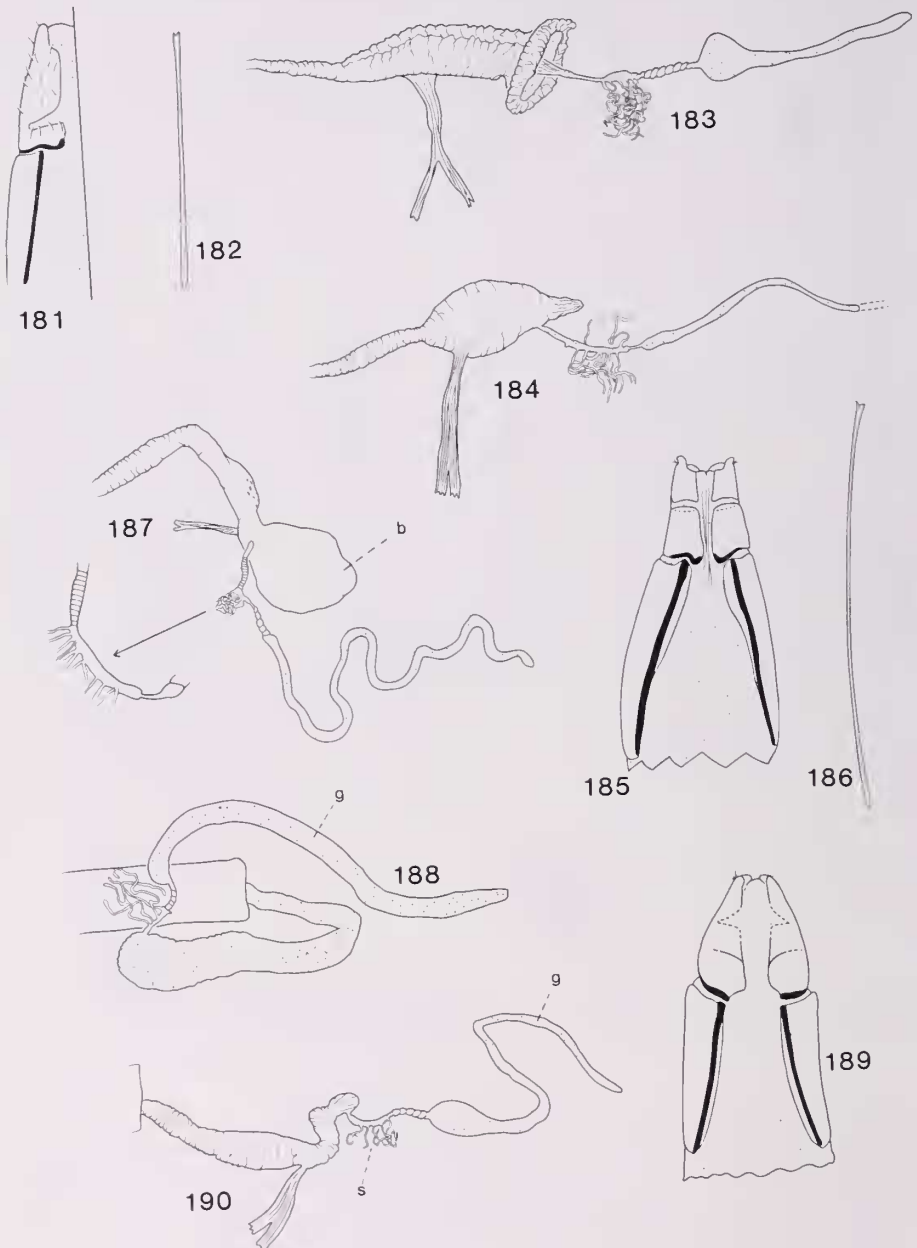
independently several times in Pimeliinae (and many times in non-Pimeliinae), and that interpretation of these characters is subject to great homoplasy. In this analysis I have considered only the elytral-sternal junction, feeling that at this time the variation in the elytra-elytra joint requires much more analysis to be useful as a taxonomic character. Although Fiori examined far too few genera to allow any meaningful taxonomic conclusions, his detailed study was seminal in pointing to a set of potentially valuable characters which has been almost completely neglected. Besides the mechanisms considered here, the elytra also interlock with the scutellum and the thoracic pleurites. Fiori also pointed out the unique interlock between the elytra and pronotum of *Erodius* (see Char. 33 above).



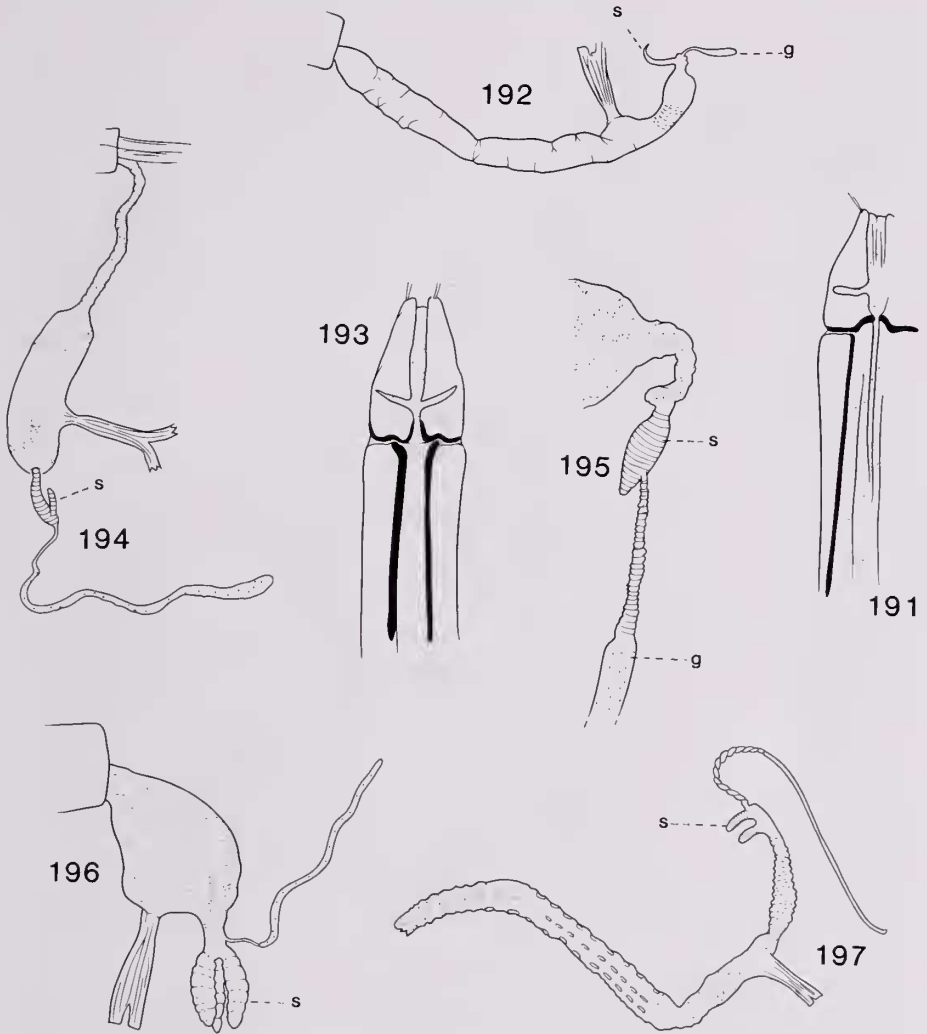
Figs. 172–180. Female genitalia of Thinobatini and Eurymetopini. 172. Internal tract of *Arthroconus fuscus* (Solier); 173–175. Ovipositor, spiculum and detail of female tract of *Thionobatis rufipes* Solier; 176–178. Ovipositor, spiculum and internal tract of *Trientoma puertoricensis*; 179. Internal tract of *Achanius* sp. (Natal, Brazil); 180. Internal tract of *Ambigatus* sp. (Natal, Brazil). b = bursa copulatrix; g = accessory gland; s = spermatheca.

Enlarged abdominal laterotergites (Char. 80), especially on the basal sternites are mostly involved with amplexiform coupling with the elytra, but occur in a few taxa with other means of elytral-sternal interlocking.

Aedeagal orientation is of the inverted type (derived) in all Pimeliinae which have been examined except *Alaudes*, which has the 'normal' orientation found in all non-



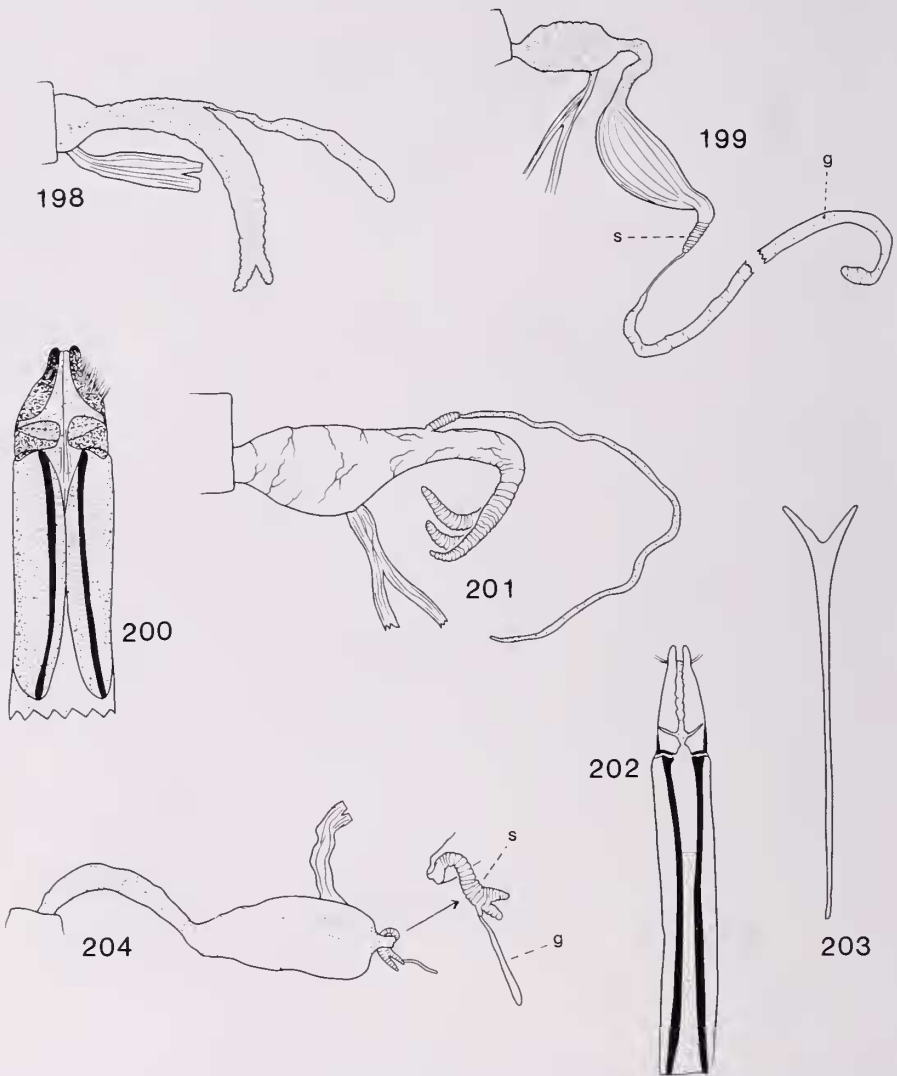
Figs. 181-190. Female genitalia of Eurymetopini. 181-183. Ovipositor (ventral), spiculum and internal tract of *Mencheres elongata* Champion; 184. Internal tract of *Cryptadius inflatus* LeConte; 185-187. Ovipositor, spiculum and internal tract of *Edrotes ventricosus* LeConte; 188. Internal tract of *Ascelosodis concinnus* Bates; 189-190. Ovipositor and internal tract of *Chilometopon pallidum* Casey. b = bursa copulatrix; g = accessory gland; s = spermatheca.



Figs. 191–197. Female genitalia of Tentyriini. 191, 192. Ovipositor (ventral) and internal tract of *Nerina furcilabris* (Fairmaire); 193, 194. Ovipositor and internal tract of *Derosphaerius anthracinus* Westwood; 195. Internal tract of *Tentyria moroccana* Solier; 196, 197. Internal tracts of *Mesostena angustata* Fabricius and *Himatismus* sp. (Thabazimbi, Transvaal). g = accessory gland; s = spermatheca(e).

Pimeliinae except *Zolodinus*. In the cladograms the condition in *Alaudes* appears as a reversal.

Several tribes of Pimeliinae have distinctive antennal form (Chars. 82, 83), but the states of these characters are obviously subject to homoplastic interpretation because of their simple nature. This is also reflected in the large number of state



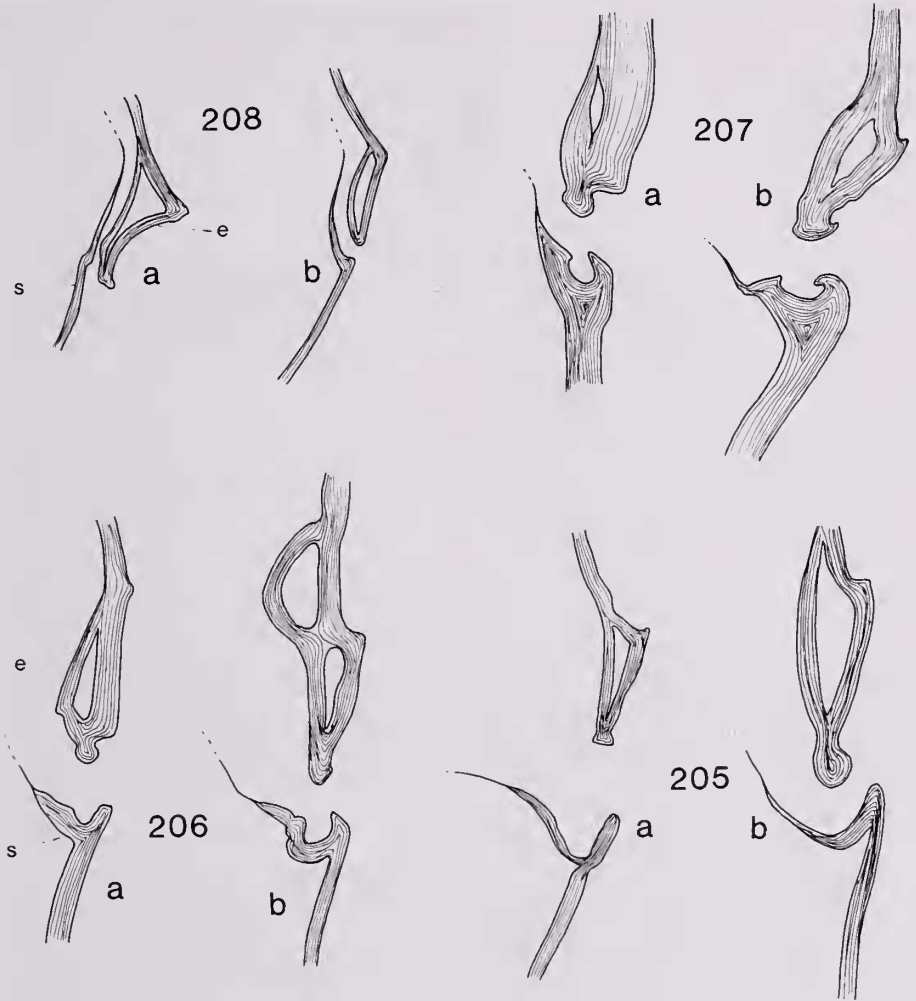
Figs. 198–204. Female genitalia of Adesmiini and Tentyriini. 198, 199. Internal tracts of *Onymacris plana* Peringuey and *Epiphysa flavicollis* Fabricius; 200, 201. Ovipositor (ventral) and internal tract of *Adesmia chiyakensis*; 202–204. Ovipositor, spiculum and internal tract of *Eptirichia tsendsureni* Kaszab. g = accessory gland; s = spermatheca(e).

changes (Char. 83). Antennal sensoriae, very useful in higher classification of non-Pimeliinae, are invariant in Pimeliinae, always consisting of sensillae basiconicae.

#### CLADOGRAMS

With a set of all primitive character states (HYPO) specified as out-group, ten equally parsimonious cladograms resulted (c.i. = 0.18; r.i. = 0.56; l = 743). With





Figs. 205–208. Cross sections of elytra and abdominal sternites, showing types of interlocking. 205. Type of joint typical of flighted forms; a. *Eupsophulus castaneus*; b. *Gyriosomus foveipunctatus* Fairmaire; 206. Open tongue and groove joint; a. *Edrotes ventricosus*; b. *Tentyria moroccana*; 207. Closed tongue and groove joint; a. *Heterasida bifurca* LeConte; b. *Pimelia* sp. 208. Amplexiform joint; a. *Brinkia debilis* Peringuey; b. *Phlagra* sp. (Grahamstown, South Africa). e = epipleural ridge; s = sternite; the laminar structure of the cuticle is shown diagrammatically; the single line becoming dashed indicates the membranous tergum.

Belopini specified as out-group eight equally parsimonious cladograms resulted (same tree statistics). With *Zolodinus* specified as out-group four equally parsimonious trees were obtained (c.i. = 0.19; r.i. = 0.56; l = 734). The length of the last set of trees is reduced because the data set included one less taxon when *Zolodinus* was designated the out-group. If the hypothetical primitive OTU is left in the data set with *Zolodinus* as out-group, then the shortest tree length obtained is 743 and the c.i. is 0.18.

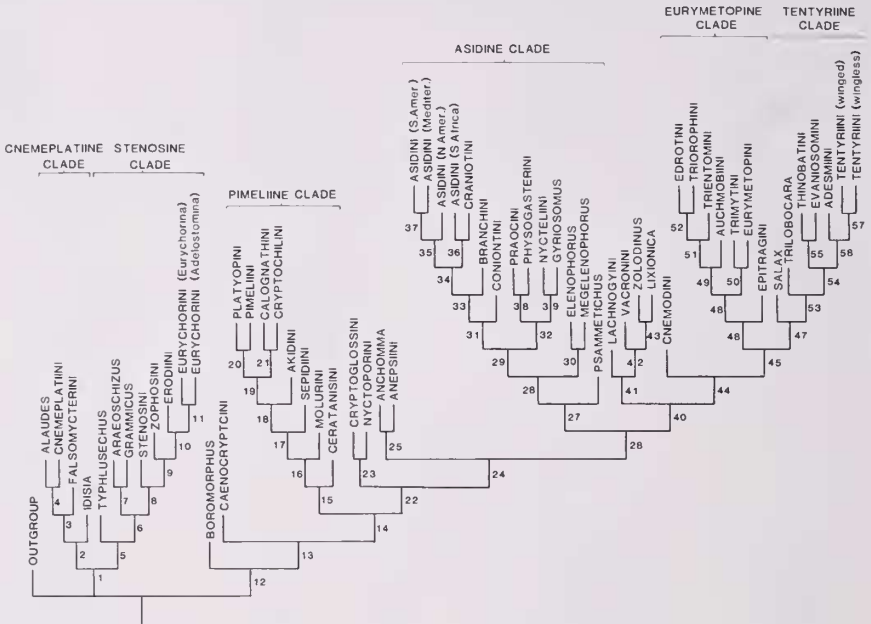


Fig. 209. Cladogram rooted by hypothetical out-group of all primitive character states. Taxa include genera of uncertain affinity as well as tribes. Numbers on stems refer to synapomorphies listed in Table 1. Characters and states are described in Appendix 2. States for each taxon are listed in Appendix 3. The number of steps, consistency index and retention index for each character are listed in Appendix 4. Total tree length = 743; c.i. = 0.18; r.i. = 0.56.

All the major clades show very high congruence over all the trees, but their positions relative to the base of the tree change, of course. One of the ten trees obtained with the hypothetical out-group is illustrated, along with consensus results (Figs. 209, 210). One of the four trees resulting from using *Zolodinus* as out-group is illustrated (Fig. 211). Only the consensus tree resulting from using *Belopini* as out-group is shown (Fig. 212; c.i. = 0.18; r.i. = 55; l = 761). Major aspects of cladogram topology are discussed below. Character changes, characterization of individual clades and relationship to classification are discussed later.

Six major clades are evident in all the cladograms, and the positions of nearly all taxa within these clades are constant. A few outlying taxa shift position unpredictably; most of these have previously been recognized as systematic problems.

With a hypothetical out-group specified, the cnemeplatiine and stenosiine clades are basal. The combined cnemeplatiine-stenosiine lineage is defined by only two synapomorphies, but taxa within each individual clade have five defining synapomorphies. The basal taxa of the stenosiine clade change position in the various cladograms, and much of the structure of Fig. 209 disappears in the consensus cladogram (Fig. 210). If *Zolodinus* is specified as out-group the position of the cnemeplatiine-stenosiine lineage changes (Fig. 211), but the included taxa are almost exactly the

Table 1. Character state changes for Figure 209, listed by stem number. Characters and states are described in Appendix 2.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
59.1	3.2	30.1	1.2	51.2	15.2	18.1	49.2	16.3	39.1	15.1	57.2	30.3	34.1	23.1	36.2
60.1	18.1	55.1	14.3	52.2	22.1	82.2	59.2	19.2	43.2	22.3	58.2	32.1	53.2	49.2	54.2
	47.2		16.3	79.1	45.2			20.2	73.3	26.2	65.2	50.2		59.3	
	83.1		41.5	83.3	65.3			24.2	80.1	27.2		51.2		64.2	
								25.2	82.2	46.1				67.1	
								28.3	83.5	52.1					
								32.3		55.1					
								50.2		62.2					
								60.2		66.2					
										69.3					
										70.2					
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
28.3	23.2	36.1	1.2	3.2	23.3	24.2	65.4	22.1	24.2	19.2	65.3	23.2	36.2	22.3	24.1
43.2	42.3	37.2	2.2	15.2	67.4	28.3	70.2		49.2	28.3	67.2	38.1	69.3	53.1	40.2
55.1	59.2	39.1	18.1	25.2	68.1	41.5	76.3		54.2	79.1	69.3	39.1	80.1	64.6	
79.1	62.2	58.1	26.2	33.3	75.2						73.1	52.2			
			31.1	34.2								67.1			
			64.3	41.5											
			72.2	46.3											
				57.1											
				62.1											
				64.4											
				80.2											
				82.3											
33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
59.4	0.2	18.1	34.2	65.2	21.2	57.1	30.1	23.1	24.1	15.2	16.4	9.2	52.2	9.3	49.1
60.3	25.2	55.1	42.1		23.1			59.3	50.1	30.2	20.2	11.2	62.4	10.3	54.1
61.3	57.1	69.1			64.6				78.1	67.3	22.1	29.1		67.3	
83.1	58.1									69.3	25.2	32.3			
	80.1										34.2				
	82.2										78.1				
49	50	51	52	53	54	55	56	57							
42.3	39.1	9.3	17.2	52.2	64.1	10.2	66.2	48.1							
78.3	58.1	10.3		65.3	65.2	49.1		74.3							
79.3				67.2	70.1	54.1									
				68.3		76.1									
				75.1											
				76.2											

same. The only exception is *Falsomycterini*, which on two of the trees with *Zolodinus* as out-group appears in a basal trichotomy with *Zolodinus* as sister to all other taxa (Fig. 211). In the other two cladograms with the same out-group *Falsomycterini* joins the *cnemeplatiine* clade distal to *Idisia*. In all four of these cladograms the *cnemeplatiine-stenosine* lineage occupies a derived position, coordinate with the *pimeliine* clade. With *Belopini* specified as out-group the *cnemeplatiine-stenosine* lineage is basal, but does not include *Falsomycterini*, which appears among a group of single taxa at the base of the combined *eurymetopine-tentyriine-asidine* clades (Fig. 212). In this cladogram *Idisia* appears at the base of the *stenosine* clade, rather than at the base of the *cnemeplatiine* clade, and the positions of several taxa show minor changes within the *stenosine* clade.

The *pimeliine* clade occupies a relatively *plesiomorphic* position with *HYPO* or *Belopini* as out-groups; in the cladogram with *Zolodinus* as out-group it holds a derived position coordinate with the *stenosine* clade. One tribe, *Caenocrypticini*, joins the *pimeliine* clade when the out-group is *Zolodinus* or *Belopini*; with *HYPO* as out-group *Caenocrypticini* occupies an isolated, *plesiomorphic* position near *Boromorpus*. In all cladograms the other taxa included in the *pimeliine* clade are identical and their relative positions show slight variation.

The *asidine* clade contains 14 taxa when *HYPO* is specified as the out-group (Fig. 209). If *Zolodinus* is the out-group the taxon pairs *Cryptoglossini* + *Nyctoporini* and *Anepsiini* + *Anchomma* join the *asidine* clade in a relatively basal position (Fig. 211). With *HYPO* as out-group both pairs branch separately just apical of the *pi-*

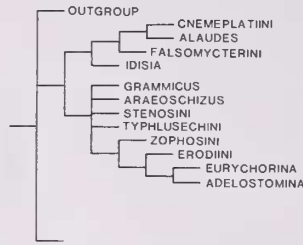


Fig. 210. Nelsen consensus for 10 trees obtained with hypothetical out-group. The only changes from Figure 209 are in the stenosine clade, shown here. Total tree length = 749; c.i. = 0.18; r.i. = 0.56.

meliine clade. With Belopini as out-group only Cryptoglossini + Nyctoporini joins the asidine clade (Fig. 212). The 14 core taxa that appear in the asidine clade in all cladograms always bear the same topological positions, and this clade is not modified in consensus trees.

The eurymetopine + tentyriine clades + Cnemodini form a stable unit which appears unchanged in all cladograms. The position of the combined clade varies, however, from relatively plesiomorphic with *Zolodinus* as out-group to derived with Belopini or HYPO as out-group. With HYPO as out-group Lachnogyiini, Vacronini and Zolodinini appear as outliers of the eurymetopine-tentyriine clade but with the other out-groups they have remote positions.

A few taxa have unstable relationships depending on the out-group. Lachnogyiini and Vacronini have already been mentioned above. In addition, *Boromorphus* always appears as a singleton while Falsomycterini shows major shifts of position among different cladograms. Finally the pairs Cryptoglossini + Nyctoporini and Anepsiini + *Anchomma* occupy rather divergent positions. The positions of most of these have previously been a matter of contention.

The consistency indices obtained here are low compared to many reported values. As shown empirically by Archie (1989a, b), however, and by Klassen et al. (1991) for random data sets the c.i. is inversely correlated with the number of taxa analyzed. Based on their scatterplots of data from the literature, a c.i. value of 0.18 is well above the expected average for data sets as large as those analyzed here. Higher values have been obtained for some large data sets, however (e.g., Loconte and Stevenson, 1991: 57 taxa, 107 characters, c.i. = 0.29).

The low consistency indices experienced with the large data sets reflect a high level of homoplasy, of course. In the present study, nearly all characters are homoplastic (Appendix 4). By recoding convergent conditions as separate states or as different characters homoplasy could be reduced and the c.i. increased considerably. For example, in Fig. 209 state 3 of character 28 (thickening of the rim of the oral foramen) occurs in stems 28 (asidine clade) and 17 (pimeliine clade). These clades are distinct and stable in all cladograms and are distinguished by numerous other characters. It is highly likely that the thickened foraminal rim is a convergence associated with armoring of the body in general and increased integrity of the mouthpart sclerites in particular. This likelihood is, perhaps, increased by differences in associated structures

such as the mentum and submentum. Nevertheless it remains impossible to distinguish more than a single character state based only on the features of the oral rim. Similar considerations attend many other characters, such as closure of the mesocoxal cavities, position of the gonostyles on the ovipositor coxites, shape of the transverse bridge of the tentorium, etc. However, when retained in the character data, homoplasy serves the function of flagging the features in which convergences might be expected. Conversely, recoding these characters would raise the consistency index without changing the cladogram or improving its reliability. For these reasons, the original character state coding was retained in all analyses.

Using HYPO as out-group the data were analyzed using the successive weighting option of Hennig86. The consistency index was greatly increased (to 0.43 after one cycle of weighting), but the number of trees found in subsequent cycles increased to over 1,600, overflowing the storage limits of the program. Thus, while homoplasy was reduced, decisiveness (*sensu* Goloboff, 1991) was lost.

Selected characters with low c.i. and r.i. were individually deleted in Hennig procedures using HYPO as out-group, resulting in marginal increases in c.i. and moderate changes in tree topology. If the seven characters (#s 15, 22, 40, 42, 43, 45, 80) are inactivated the tree length decreases to 637, c.i. increases to 0.20, while the number of equal length trees increases to 124. In some of these trees several taxa from the stenosine clade shift onto the cnemeplatiine clade and the pimeliine clade loses Molurini, Sepidiini and Ceratanisini. The large asidine, tentyriine and eurytmetopine clades are stable except for a few minor changes and *Zolodinus*, *Lixionica* and *Vacronini* remain at the base of the combined tentyriine-eurytmetopine clade. I interpret these results to indicate that even the characters of low c.i. in this data set are important in determining cladogram topology and stability. Removing these characters lowers the decisiveness of the data by increasing the number of trees, while scarcely influencing consistency. This is not to imply that all the cladistic groupings in Figures 209–212 are unchangeable. Some clades, such as the stenosine are much more weakly supported than others, such as the asidine. Likewise, the positions of some taxa (such as *Zolodinini*) are relatively unstable. These taxa and the reasons for their problematic composition or position are discussed in more detail below.

#### TAXONOMIC INTERPRETATIONS

**Position of *Zolodinini*.** The sister taxon of Pimeliinae has been a matter of some disagreement. Based on its internally and externally open procoxal cavities, lack of defensive glands and inverted aedeagus, Watt (1974) placed *Zolodinini* as sister to Pimeliinae. The larva of *Zolodinus*, described by Watt, appears to be primitive compared to those of Pimeliinae, and Watt did not specify larval synapomorphies linking the two.

In their analysis of cladistic structure of the major tenebrionid lineages other than Pimeliinae, Doyen and Tschinkel (1982) suggested that *Zolodinini* might represent a specialized derivative of some other lineage. Most of the similarities shared with Pimeliinae are either primitive characteristics or convergences; the most convincing synapomorphy is the inverted aedeagus. A shortcoming of both studies was the abbreviated treatment accorded Pimeliinae. Watt mentioned details of only two other taxa, *Nyctoporini*, which he believed to represent a relatively primitive tribe, and *Pimeliini*, which he dismissed as a specialized derivative of the tentyriine clade. Both



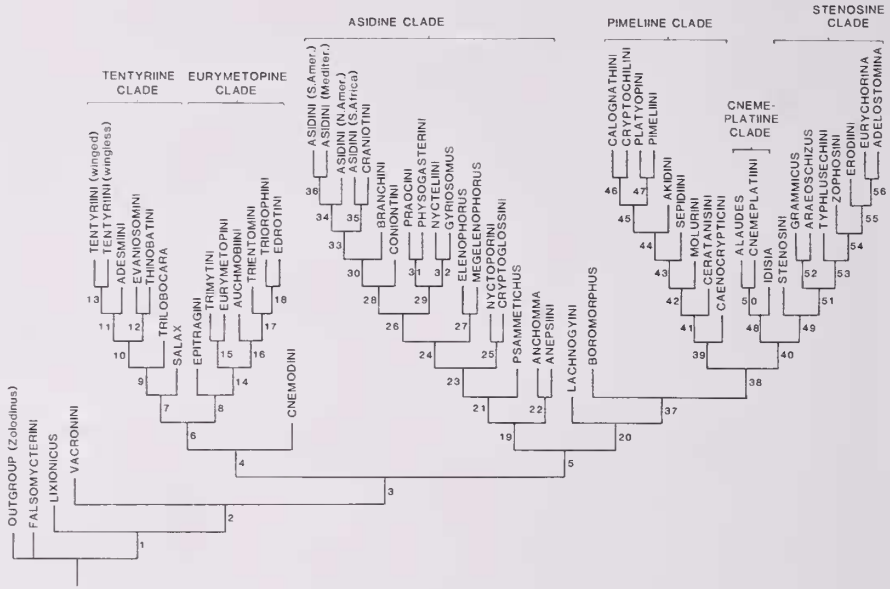


Fig. 211. Cladogram based on *Zolodinus* as out-group. Conventions as for Figure 209. Characters and states are listed in Table 2. Total length = 734; c.i. = 0.19; r.i. = 0.56.

these placements are refuted below. Doyen and Tschinkel examined only about a dozen relatively derived genera of Pimeliinae, representing few tribes in the large pimeliine, asidine, eurymetopine and tentyriine clades. Based on the present analysis, several of the character states they designated as primitive to the pimeliine clade were incorrect.

Comparison of Figures 209–212 reveals a basic difficulty in classifying Zolodinini as sister to Pimeliinae. If a hypothetical out-group of all primitive character states is designated (Fig. 209), then Zolodinini clusters at the base of the highly derived eurymetopine-tentyriine clade, a group which was also considered apomorphic by Watt (1974). Designating Belopinae as out-group likewise relegates Zolodinini to a relatively derived position. Only by designating Zolodinini as the out-group can it be forced into the sister group status. When this is done the cnemeplatiine clade, here considered primitive is moved to a highly derived position (Fig. 211). Examination of *Zolodinus* adults reveals a number of apomorphic features such as the sclerotized ovipositor with lateralized gonostyli and the structure of the internal female reproductive tract, which has numerous, extremely fine, apparently unbranched spermathecal tubes. These diverge individually from a common duct attached at the base of the spermathecal accessory gland (Tschinkel and Doyen, 1980: fig. 47), an arrangement which is vaguely similar to that of the asidine clade. In the asidine tribes, however, the spermathecal tubes are much thicker and many fewer, and usually branch from the common duct at a single point (Figs. 125, 128, 132–138, 140–143). Numerous, very fine spermathecal tubules occur in some Adeliini (e.g., *Adelodemus*), but that tribe differs in numerous other features and could not be close to Zolodinini.

Table 2. Character state changes for Figure 211. Characters and states are described in Appendix 2.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
57.2	15.1	24.2	16.4	16.1	9.2	9.3	52.2	42.3	65.2	42.2	10.2	18.1	49.1	39.1	42.3
58.2	67.4	50.2	20.2	18.2	11.2	10.3	62.4	52.2	70.1		51.1		54.1	58.1	78.3
67.3	69.1		22.1	78.3	18.2	67.3		65.3							
			23.3		25.2			67.2							
			34.2		29.1			68.3							
			46.2		30.3			76.2							
					32.3										
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
9.3	17.2	30.3	24.1	19.2	49.1	65.3	67.2	41.5	23.2	34.2	22.3	24.1	59.4	21.2	57.1
10.3		23.3	32.2	28.3	54.1		69.2	70.1	38.1	36.2	53.1	40.2	60.3	23.1	58.1
			34.2	79.1	58.1		73.1	76.2	39.1	69.3	64.6		61.3	59.3	76.2
			53.1		59.1				52.2	80.1	67.1		83.1	64.6	
			80.3												
33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
0.2	18.1	34.2	65.2	49.1	24.1	30.3	50.1	34.1	53.2	28.3	42.3	36.1	3.2	1.2	3.2
25.2	19.1			54.1	39.2	32.1	57.1	64.2		43.2	62.2	37.2	33.3	2.2	18.1
57.1	69.1			65.2	68.3	36.2	58.1	67.1		55.1		58.1	34.2	26.2	47.2
58.1				67.2	75.1		60.1			80.1			41.5	31.1	51.1
82.2				70.1	76.2								46.2	64.3	55.1
													80.2	77.1	59.1
													82.3		65.1
49	50	51	52	53	54	55	56								
15.2	1.2	52.2	18.1	24.2	16.3	39.1	15.1								
22.1	14.3	80.2	43.2	28.3	20.2	43.2	26.2								
65.3	16.3	82.2	59.1		25.2	45.2	27.2								
79.1	30.1				32.3	73.3	46.2								
83.3	41.5				49.2	80.1	52.1								
					50.2	83.5	55.1								
					83.4		62.2								
							69.3								
							70.2								

*Zolodinus* is similar in many adult features to *Vacronini*, near which it appears in the cladograms, but larval differences seem to preclude a close relationship. Larvae of *Zolodinus* are similar to generalized forms such as *Tenebrio*, while larvae of *Vacronini* are similar to those of *Epitragini*, *Trimyitini* and related tribes, with greatly enlarged forelegs and mandibles bearing basolateral tufts of stout setae (Doyen and Lawrence, 1979). Larvae of the less specialized tribes of the *cnameplatiine* and *stenosine* clades are known only from *Dichillus* and *Stenosus* (Keleynikova, 1976), and *Idisia* (Hayashi, 1966), which all have moderately enlarged forelegs and mandibles with only a few stout basolateral setae. The larva of *Vernayella* is similar (Endrödy-Younga and Doyen, in preparation) and larvae of this type may represent the primitive body plan for *Pimeliinae*. If tribes such as *Cnameplatiini* and *Stenosini* represent primitive *Pimeliinae*, then it seems highly unlikely that *Zolodinini* is the sister group of *Pimeliinae*, based on the cladograms discussed above. The most likely alternative is that the apomorphies shared by *Zolodinus* and *Pimeliinae* (inverted aedeagus and lack of defensive glands) are convergent. A few other tribes have apparently lost the defensive glands (*Phrenapatini*, *Goniaderini*, *Chaerodini*), and in some *Cyphaleini* the reservoirs are extremely small. Inversion of the aedeagus is unknown among other non-*Pimeliinae*, but *Alaudes* (*Cnameplatiini*) is unique among *Pimeliinae* in having the aedeagus in the normal position. Because of the complexity of these sometimes contradictory character distributions it seems best to reserve judgement on the position of *Zolodinini* until the relationships of the entire family can be reanalyzed.

*Lixionica* Blackburn (= *Exangelus* Blackburn) clusters near *Zolodinus* in all cladograms, but its placement is problematic. Kaszab (1977) placed *Lixionica* in *Ceratanisini*, which it resembles in external characters. The internal female reproductive

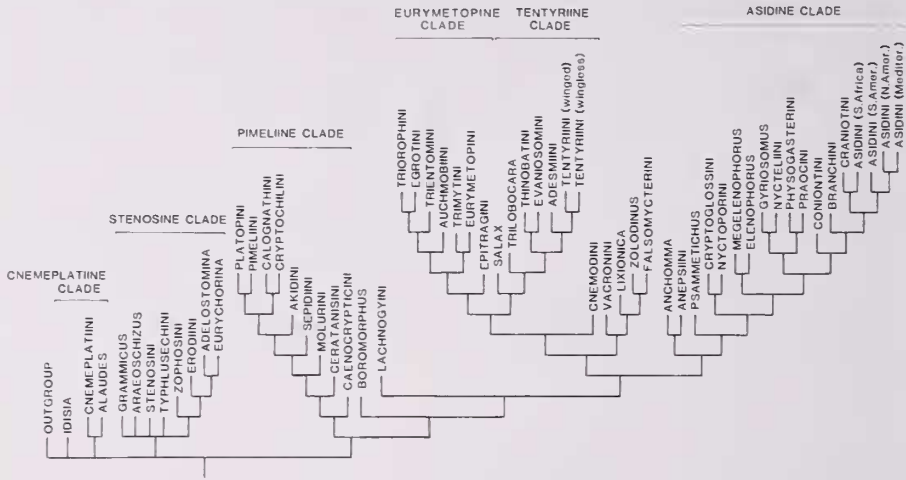


Fig. 212. Cladogram based on Belopini as out-group. Total length = 746; c.i. = 0.18; r.i. = 0.55. Character changes not shown.

tract, however, resembles the type found in the eurymetopine clade, with spermathecal tubules branching individually from the base of the accessory gland. The internal closure of the procoxal cavities (Character 30: 1) is also of the eurymetopine type. In Ceratanisini the internal female tract is autapomorphic (Fig. 80), but the ovipositor is similar to that of Akidini (Figs. 78, 83), with a distinct gonostyle set in a large membranous oval window in the sclerotized coxite; procoxal closure is of the asidine type (Char. 30: 3). The ovipositor of *Lixionica* is similar to that of *Nyctoporis* and *Alaephus*, with mostly generalized features. Based on the features cited above *Lixionica* is tentatively placed in Vacronini. Discovery of the larva, however, may dictate a different position.

**Cnemeplatiine Clade.** This lineage includes only a few genera, listed below. It is defined by five synapomorphies in Fig. 209. Reduced size of tentorium (3: 2) occurs convergently in Cryptochilini, but is otherwise unique to the cnemeplatiine clade. Consolidation of the submentum with the gula (18: 1) occurs also in *Araeoschizus* and *Grammicus* (stenosine clade) and in Pimeliini. Reduced ovipositor and spiculum (47: 2) do not appear elsewhere as a synapomorphy, but occur in *Araeoschizus* (stenosine clade). Clubbed antennae (83: 1) occur sporadically in many different Pimeliinae (see Appendix 3), but appear as a synapomorphy only in the cnemeplatiine (stem 2) and asidine (stem 33) clades. The clubbed antennae of the asidine tribes, much longer relative to body size, with a differently formed club with large sensory patches, are certainly convergent.

*Idisia* is differentiated from other members of the cnemeplatiine clade in having externally open procoxal cavities (31: 1) and very short spiculum (55: 1) in the female. Externally open procoxal cavities occur in Zolodinini, apparently as a primitive feature. Open cavities also occur in some Pimeliini, Platypini and Cryptochilini, but probably as a secondary condition (see character analysis). The open condition

was coded as primitive in *Idisia*, but could well be secondary, since in all other Tenebrionidae external closure precedes internal closure.

Because of its numerous specialized features apparently related to myrmecophily, *Alaudes* was entered as a separate taxon in all analyses. It uniformly clusters with Cnemeplatiini, with which it shares six synapomorphies. One of these (14: 3) is unique; the others occur also in Pimeliini (1: 2; stem 20), Eurychorini, Erodiini and Zophosini (16: 3; stem 9) and Cryptochilini (41: 5; stem 21). All these other taxa differ in many important features, and it seems clear that *Alaudes* belongs in Cnemeplatiini.

With Zolodinini as out-group (Fig. 211) *Falsomycterus* drops out of the Cnemeplatiini clade, clustering at the base of the cladogram, coordinate with Zolodinini. The reduced cnemeplatiine clade (stem 48) is defined by seven synapomorphies. In this cladogram *Alaudes* and Cnemeplatiini share seven additional apomorphies. These synapomorphies are mostly the same as those on Fig. 209, in slightly different arrangement.

With Belopini as out-group both *Falsomycterus* and *Idisia* drop out of the cnemeplatiine clade (Fig. 212). *Falsomycterus* appears near *Zolodinus*, while *Idisia* is located at the base of the stenosine clade.

The cnemeplatiine genera are included under Opatrini in most catalogs, but Csiki proposed the tribe in 1953 and for some time specialists have recognized it as a member of Pimeliinae (Medvedev, 1968, 1973; Doyen and Lawrence, 1979; Doyen et al. 1989). Besides *Cnemeplatia* Costa and *Lepidocnemeplatia* Kaszab, Cnemeplatiini should contain *Thorictosoma* Lea (transferred from Opatrinae by Doyen et al., 1989), *Actizeta* Pascoe and *Philhammus* Fairmaire (transferred by Watt, 1992) and *Alaudes* Horn (hereby transferred). The first two genera are widely distributed, while *Thorictosoma* is endemic to Australia, *Actizeta* to New Zealand and *Alaudes* to western North America, all in seasonally or edaphically arid situations. *Philhammus* occurs in the Mediterranean region and in Armenia.

Watt (1992) detailed the morphological characteristics of several cnemeplatiine genera and described the larva of *Actizeta albata* Pascoe. He proposed that Cnemeplatiini are the sister taxon to all other Pimeliinae. Although he did not mention the stenosine clade, his results are clearly in accord with those presented here.

*Idisia* and *Falsomycterus* are phenetically quite different from Cnemeplatiini and should remain as separate tribes. Medvedev (1973) suggested that *Idisia* was close to Cnemeplatiini when he proposed Idisiini, citing similarities in male genitalia and mouthpart structure, without mentioning specific characters. Male genitalia are of rather simple structure as in most Pimeliinae. Mandibles do not have the molar lobe strongly reduced and modified in as *Lepidocnemeplatia* and *Alaudes* (less so in other Cnemeplatiini) and are generalized in the other features considered here. Moreover, *Idisia* does not always appear in the cnemeplatiine clade, depending on the out-group designated, and could justifiably be placed at the base of the stenosine clade.

*Falsomycterini* appears as a member of the cnemeplatiine clade only with HYPO as out-group. Doyen and Lawrence (1979) mentioned a peculiar secondary sexual feature (a mental gland) shared by male Anepsiini and *Falsomycterini*, but the present analysis does not support a close relationship. Among the more unusual falsomycterine features are the female tract which has multiple spermathecae (Figs. 69, 71) combined with a balloon-like gland. Enlarged, saccate glands occur in a few members

of the stenosine clade (Eurychorini, some Zophosini; Figs. 53–55, 71) and in *Ver-nayella* (Fig. 77), but these taxa differ in numerous other features. The mandibles of *Falsomycterini* are long and falciform. The apicale of the aedeagus bears a strong, slightly hooked tooth dorsally near the middle. The procoxal cavities are closed externally by a very broad postcoxal bridge and open internally. The multiple spermathecae are one of the characters causing *Falsomycterus* to cluster with *Zolodinus* in some analyses. The spermathecal tubes in *Pteroctenus* are long and slender (Fig. 69) as in *Zolodinus*, while those of *Falsomycterus* (Fig. 71) are much shorter and thicker. *Pteroctenus* and *Zolodinus* also differ greatly in ovipositor structure (Figs. 66, 67). In *Falsomycterus* the ovipositor is rudimentary. Thus, *Falsomycterini* cannot confidently be placed in any of the lineages discussed here, and must be accorded an isolated position in Pimeliinae.

**Stenosine Clade.** This lineage joins basally with the cnemeplatiine clade except when *Belopini* is designated as out-group. With a hypothetical out-group (Fig. 209) only two characters define the combined cnemeplatiine-stenosine clade, both involving ovipositor proportions. With *Zolodinus* as out-group, the combined lineage is defined by four synapomorphies (Fig. 211, stem 40), all characters of the ovipositor. In the classification of Gebien (1938–1942) and LeConte (Leng, 1920) the stenosine tribes were included in Asidinae, except for *Erodiini* and *Zophosini*, which belonged to Tentyriinae. The characters of the female reproductive tract strongly differentiate the stenosine group from Gebien's Asidinae, and all but *Erodiini* from Tentyriinae. In the Asidinae the female tract has multiple, fasciculate, tubular spermathecae attached either to the base of the spermathecal gland or to the bursa near the gland base (Figs. 140–143). In the stenosine groups the spermatheca is compact, either capsular or short-tubular and either single or, uncommonly, once branched (Figs. 40, 43, 46, 53–55). It shares a common duct with the spermathecal gland (Figs. 53–55) or appears as a differentiated part of the bursa to which the gland attaches (Fig. 40). *Anchomma*, originally associated with *Colydiidae* and later moved to *Stenosini* (Doyen and Lawrence, 1979), properly belongs in *Anepsiini* (see below).

The stenosine lineage has constant membership in all cladograms, with the exception of *Idisia*, which joins the cnemeplatiine clade in one arrangement with *Belopini* as out-group. The positions of the more basal taxa are variable, and in the consensus trees *Granmicus*, *Araeoschizus*, *Stenosini* and *Typhlusechini* all arise separately from the primary stenosine stem (Figs. 210, 212). Thus it would seem advisable to combine *Araeoschizini* and *Typhlusechini* under *Stenosini*, possibly as subtribes. The more specialized members of the lineage, however, are constant in position over all cladograms.

The basal stenosine stem is defined by four or five synapomorphies except in the consensus tree, where the synapomorphies from several dichotomies are compressed into the basal stem. None of the individual synapomorphies are unique, and changing the out-group changes the synapomorphies (only 79: 1 and 83: 3 are common to all analyses). The stenosine lineage is thus distinguished in part by lacking the more obvious synapomorphies involving mouthparts and the internal female genital tract which characterize the asidine, etc. clades.

The more derived members of the stenosine clade (*Zophosini*, *Erodiini*, *Eurychorini*) maintain the same position in all cladograms. *Zophosini* and *Erodiini* are structurally among the most specialized Tenebrionidae, but their specialized features



are very largely autapomorphic and do not influence the tree topology. However, each dichotomy is defined by numerous synapomorphies and several of these appear regardless of out-group. These synapomorphies represent many different organ systems and body regions. Overall this must be considered one of the best supported parts of the cladogram.

The members of Zophosini are strongly canalized for an active, heliotactic style of life, notably for extremely rapid running and the ability suddenly to change direction. This is facilitated by the reduction of the abdomen and the conformation of the entire thoracic-abdominal region into a rigidly joined attachment surface for the large coxal and trochanteral muscles which power the abrupt movements. Structural integrity of the thoracic-abdominal region is further increased by fusions of endoskeletal elements. Penrith (1986a), based on the high degree of similarity in external features, placed all Zophosini into the single genus, *Zophosis*. The internal female reproductive tract of Zophosini, however, shows remarkable variation (Figs. 58–65). While a condensed classification of Zophosini may prove desirable, a survey of the female tract over all subgenera of *Zophosis* (only four investigated here) is obviously needed.

The position of Eurychorini as the most derived member of the stenosine clade may seem surprising, since many eurychorine taxa, particularly of the Adelostomina, seem less specialized than Zophosini or Erodiini. Koch (1955: 24), however, recognized the highly derived nature of Eurychorini, and also suspected that they were related to Stenosini. One synapomorphy uniting Stenosini and Eurychorini is the form of the spiculum ventrale, which has the basal arms subequal to the stem (Fig. 52).

Erodiini fits least easily into the stenosine clade. The internal female reproductive tract of Erodiini includes a short, saccate accessory gland (Figs. 56–57). The bursa is differentiated as a small, attenuate appendage ("spermatheca") in *Erodius*, superficially similar to the more strongly differentiated spermathecae of Tentyriini and Adesmiini, especially genera such as *Nerina* (Fig. 192) and *Stenosida*. In the last two the accessory gland is also short and saccate, as in Erodiini, whereas in most Tentyriini the gland is long-tubular. In Erodiini, however, the ovipositor has specialized, spatulate apical coxite lobes (simple in Tentyriini, Figs. 191, 193) and the spiculum has long basal arms (as in Fig. 163; arms shorter in Tentyriini, Fig. 203). In Erodiini the maxillary bases are concealed entirely by the subgenal processes (Fig. 23) while in Tentyriini the maxillary socket is formed by both subgena and submentum (Fig. 24).

Larvae have been associated with Erodiini, Zophosini, Eurychorini and old world Stenosini (Keleynikova, 1962, 1976; Schulze, 1962, 1974) as well as Tentyriini (Keleynikova, 1959). Larvae of Erodiini have thick, moniliform bodies and strongly fossorial legs, apparently specializations for sand dwelling. The configuration of the ninth and tenth abdominal segments is similar to that of Eurychorini, but this may be convergent. Larvae of Zophosini also have moniliform bodies, but with very differently configured ninth abdominal tergites. Larvae of Stenosini are more generalized in gross body form, but show some highly apotypic features, such as a closed tracheal system. Details of mouthparts and legs need to be compared closely over larvae of all these tribes.

**Pimeliine Clade.** This lineage includes tribes which were placed in the Asidinae of Gebien, except for Pimeliini and Platypini, which were included in Tenebrioninae



on the basis of the exposed membranes between the apical abdominal sternites. The balance of other characters, including those of larvae, clearly places these tribes in Pimeliinae (Watt, 1974; Doyen, 1972; Doyen and Lawrence, 1979). The tribes included here in the pimeliine clade are invariant, except for Caenocrypticini, which, on two of the cladograms, joins as sister to all the other pimeliine tribes. The order of tribes within the lineage is invariant except for Ceratanisini and Molurini, which exchange positions in one cladogram. The pimeliine clade appears as sister to the combined asidine + eurymetopine + tentyriine clades when the out-group is HYPO or Belopini (Figs. 209, 212). When the out-group is *Zolodinus*, the pimeliine clade moves to a highly derived position as sister to the combined cnepletiine + stenosine clades (Fig. 211). The pimeliine clade, alone among the major lineages, is restricted to the old world, where it is especially diversified in the Mediterranean region.

Most dichotomies of the pimeliine clade are defined by four or more synapomorphies. As usual these are seldom unique, mostly involving features that are subject to widespread convergence, such as consolidation of the mouthparts, lateralization of gonostyles, sclerotization of the apical coxite lobes, etc.

The most plesiomorphic tribes of the pimeliine group are Ceratanisini and Molurini. Members of the former are winged and generalized in most external characters. *Ceratanisus*, the only genus examined in detail, has an autapomorphic internal female tract (Fig. 80), with four short, smooth spermathecal tubes and a triangular sclerite in the bursal wall. One synapomorphy shared with Akidini is the form of the apical coxite lobe, which is peripherally sclerotized, leaving a large, central submembranous area into which is inserted the relatively large gonostyle (Figs. 78, 83).

The configuration of the internal female reproductive tract is highly variable in the pimeliine clade, even in some individual tribes. In Akidini, for example, there is a single (*Morica*, Fig. 82) or multiple fasciculate (*Akis*, Fig. 86) spermatheca(e). In Pimeliini the number of spermathecal tubes varies from none (*Lasostola*, *Pimelia*; Fig. 99) to one (*Oenera*; Fig. 100) or two (*Sternoplax*; Fig. 95). Variation in Cryptochilini-Calognathini is even more extreme. In *Cryptochile* the bursa is constricted, without a distinct spermatheca (Fig. 88, 89); in *Pachynotelus dimorphus* Koch there is a single spermathecal tube, isolated from the accessory gland (Fig. 91), in *Horatoma parvula* Solier a pair of tubules (Fig. 90) and in *Calognathus* six tubules, two much larger than the others (Fig. 94). In all cases, however, other synapomorphies unite the members of these tribes. For example, all Calognathini and Cryptochilini have ovipositors with pronounced ventral cleft (Char. 53, state 2) and very large, sclerotized, upturned apical coxite lobes (64: 4) (Figs. 87, 92). Likewise, genera of Pimeliini-Platyopini share a distinctive ovipositor topology (64: 3; Figs. 96, 97) and several features of the mouthparts. An unusual character shared by Cryptochilini and some Pimeliini is the externally open procoxal cavities. As discussed earlier, the specialized thoracic form of Cryptochilini would suggest that this is a secondary feature. Thoracic form in Pimeliini is much more generalized, however, indicating a primitive character from which the Cryptochiline arrangement may have been derived.

Among the synapomorphies linking Akidini to the Pimeliini is the form of the spiculum ventrale, which has the basal arms subequal to the stem (Figs. 81, 85, 98). This configuration is unusual in Tenebrionidae (also in *Stenosus*, Cryptoglossini, Anepsiini). The spiculum form in Cryptochilini, with the stem absent (Fig. 93) appears

derived from the pimeliine type. In Sepidiini and Molurini the spiculum arms are relatively large, but are strongly reflexed, especially in the latter (Figs. 102, 105).

Members of Molurini display several notably primitive characters. The female reproductive tract of most of the genera examined has multiple spermathecae which attach to the bursal wall near the gland attachment, rather than onto the gland duct itself (Figs. 106, 109). This is essentially the same arrangement which occurs in Adeliini and Pycnocerini of the Lagriine lineage (Tschinkel and Doyen, 1980). The abdominal-sternal interlocking mechanism (79: 4) is distinct from all other Pimeliinae, as discussed previously, with the epipleural edge of the elytron overlapping the expanded sternite edge (Fig. 208), rather than dove-tailing into a groove. This mechanism must have been derived from a flighted form independently from the dove-tailing found in other tribes. It may be noted here that in *Phrynocolus dentatus* Solier interlocking is of the dove-tailed form, as in Sepidiini, which are similar to Molurini in many other characters. In this study *Sepidium* was the only representative of Sepidiini; comparison of additional genera may suggest merging of Molurini and Sepidiini, or transfer of some genera.

The present data suggest two-nomenclatural changes. Pimeliini and Platyopini share all essential features, differing in a few mouthpart characters (14, 15) the size of the accessory gland (73) and antennal form (83). Reitter (1893, 1915) distinguished his "unechte" (false) Pimeliiden (including Platyopini) from true Pimeliini by the cross-sectional shape of the 2 posterior pairs of tibiae: round or elliptical in the "false" Pimeliini; 3- or 4- angled in the "true" Pimeliini. Gebien (1938-1942) included eleven genera of the "false" Pimeliini in his Platyopini, without mentioning characters. A more broadly based comparison of pimeliine genera might show that the Platyopini comprise the primitive sister to other Pimeliini, but the present data (Appendix 3) suggest the opposite—that Platyopini are relatively derived. *Leucolaephus* Lucas has sometimes been placed in a separate tribe Leucolaephini. I have not made dissections, but based on external characters *Leucolaephus* should be included in Pimeliini.

An unusual feature of Pimeliini-Platyopini is the exposed membranes between the apical abdominal sternites (Char 77: 1). This has traditionally been considered a primitive feature, but in all the cladograms reversal to the internalized condition (77: 2) takes place in the basal stem. Subsequent reversal to the exposed condition then appears in the stem to Platyopini and Pimeliini. It therefore seems likely that the exposed membranes represent a specialized reversal, rather than a retained primitive feature.

Pimeliini are highly derived in numerous characters and in previous classifications have never been placed near the base of Pimeliinae. When Pimeliini was declared out-group in the present study (cladogram not illustrated) all the major lineages maintained their cohesiveness except the pimeliine clade. Most of the pimeliine tribes fell into three small basal lineages, while Molurini and Ceratanisini occupied isolated positions in the interior of the cladogram.

Endrödy-Younga (1989) placed Calognathini and Vansoniini as synonyms of Cryptochilini. The results presented here are in full accord with his changes. Endrödy felt that *Calognathus* was relatively derived, even though it lacks the stridulatory apparatus of all other Cryptochilini. It may be noted, however, that *Calognathus* is certainly primitive in regard to metacoxal structure (Chars. 43-45), in lacking a

mid-dorsal endocranial carina (8) and in having the metendosternite free rather than fused with the mesocoxal inflexions (40). Moreover, *Calognathus* females bear a striking superficial resemblance to *Storthocnemis* Karsh (Pimeliini). Only an exhaustive comparative study including pimeliine genera will reveal the details of cladistic structure of this group of highly specialized beetles.

**Asidine Clade.** Included here is most of the subfamily Asidinae (sensu Gebien, 1937, 1938–1942), with the addition of Physogasterini, Praocini, Branchini and Coniontini and less Zopherini (=Zopheridae) and those tribes placed here in the pimeliine clade. Even after removal of the pimeliine tribes, the asidine clade represents one of the great radiations of Tenebrionidae. This clade occurs exclusively in the New World, with the exception of Asidini and *Elenophorus*. The former has representatives in the Mediterranean region, in southern Africa and in Madagascar. Because of its widespread distribution, one would expect that Asidini would be relatively old and that it would occupy a relatively basal position within the clade. In all analyses, however, Asidini holds a highly derived position. Moreover, the stem (34: Fig. 209) basal to all the asidine taxa is defined by six synapomorphies, two of which (0: 2; 82: 2) are unique or nearly so in Pimeliinae.

*Elenophorus*, which occurs in the Mediterranean region, bears a striking resemblance to *Megelenophorus* from southern South America. The relationships of these genera were previously considered by Doyen and Lawrence (1979), who tentatively concluded that *Elenophorus* was derived from Akidini, while *Megelenophorus* was related to *Psammetichus* (also South American), based on features of the skeletal anatomy. In particular, both *Psammetichus* and *Megelenophorus* stridulate by rubbing the hind femora over the epipleuron. The additional characters examined here do not entirely support those conclusions. *Megelenophorus* and *Psammetichus* agree in the configuration of the spiculum gastrale (Figs. 127, 130), which has large basal arms, but differ in the form of the internal female tract (Figs. 128, 131). In *Megelenophorus* the tract has fasciculate spermathecae, typical of the asidine clade. In *Psammetichus* the spermathecal arrangement is serial, as in the eurymetopine clade, and the accessory gland is very short. *Psammetichus* always joins the asidine clade in a relatively basal position, and, with Pimeliini as out-group, joins Nyctoporini and Cryptoglossini in a small clade at the base of the tentyriine-eurymetopine lineage. Thus, its cladistic position must be considered problematic.

*Elenophorus* differs from both *Megelenophorus* and Akidini in the form of the ovipositor (Fig. 123) and especially in the shape of the spiculum (Fig. 124), which has a slight radial basal expansion without distinct arms. The three synapomorphies linking *Elenophorus* and *Megelenophorus* all show much homoplasy. Consequently, the relationship between these two must remain tentative, at least until additional Akidini (especially species of the phenetically similar *Cyphogenia*) can be compared.

Two small sub-clades, Anepsiini plus *Anchomma* and Cryptoglossini plus Nyctoporini, join the asidine clade when *Zolodinus* or Belopini is declared as out-group. When HYPO or Pimeliini is out-group both appear as isolated doublets at the base of the combined asidine + eurymetopine + tentyriine clades. Anepsiini have the spermathecae serially arranged on the accessory gland duct (Char. 67: 4; Figs. 116, 119) as in the eurymetopine clade, but lack the specialized eurymetopine mouthparts, and have a very different ovipositor configuration and spiculum shape (Figs. 115, 118). *Anchomma*, originally included in Colydiidae, then in Stenosini (Doyen and

Lawrence, 1979) always clusters with Anepsiini, with which it shares all important synapomorphies. These taxa are excluded from the stenosine clade, which they resemble in their unspecialized mouthparts and reduced ovipositor, by several characters, such as the internally closed forecoxal cavities, (Char. 30: 3), the primitively open mesocoxal cavities (Char. 34: 1) and the serial arrangement of spermathecae.

Cryptoglossini and Nyctoporini have the spermathecae serially arranged (67: 4) and located on the attenuate apex of the bursa rather than on the accessory gland duct (Figs. 109, 113, 122). They lack the specialized mouthpart enclosure of Eurymetopini, have very different ovipositors and spicula (Figs. 107–112; 120–121) and have the asidine type of procoxal closure (Char. 30: 3). As discussed above under "Limits of Pimeliinae," *Ammophorus* properly belongs in Scotobiini, leaving Nyctoporini monogeneric. Cryptoglossini is likewise a small, uniform group, restricted to North America and northern MesoAmerica. Despite their similarities, Nyctoporini and Cryptoglossini differ strongly in such features as gonostyle size (Char. 50), spiculum size and shape (55, 63; Figs. 108, 112, 121) and metendosternite form (41), and certainly warrant status as separate tribes.

Because of their confusing patterns of synapomorphies neither Cryptoglossini, Nyctoporini nor Anepsiini can be accommodated in the major clades and are best considered as relatively plesiomorphic derivatives as in Fig. 209.

The remaining members of the asidine clade occupy stable positions across all the cladograms. The South American tribes (Praocini, etc.) always bear a sister group relationship to the remainder of the lineage, which is North and MesoAmerican with the exception of Asidini. Branchini phenetically resemble some Praocini and Nycteliini as much as Asidini, but unquestionably are close to the latter (Stem 33 in Fig. 209 is supported by four synapomorphies; stem 31 by four). In particular, both Asidini and Branchini lack the tentorial bridge (0: 2). Doyen (1972) included Branchini in Coniontini. In retrospect it is apparent that the similarities to Coniontini are plesiomorphies. Branchini, which number only three genera and about a dozen species, could be merged with Asidini, but that tribe is well supported by at least four synapomorphies (Figs. 209, 211; stems 34 and 33, respectively). In addition all genera of Branchini share an apomorphy of the ovipositor (Char. 61: 3; Fig. 137) which is never present in Asidini. For these reasons Branchini is here recognized as a distinct tribe.

Craniotini (with the single genus *Craniotus*) is included in Tentyriinae (=tentyriine-eurymetopine clade) by Gebien (1937) and Leng (1920). Its very close relationship to Asidini is irrefutable, and Craniotini should be placed in synonymy as detailed by Aalbu and Doyen (in prep.). The sister status of *Craniotus* and South African Asidini is unexpected and difficult to explain. Craniotini and African Asidini share two synapomorphies, sternal closure of the mesocoxal cavities (34: 2) and shortening of the dorsal arm of the mesendosternite (42: 1). The former is an unusual character which usually occurs in tenebrionids of small body size; the latter is strongly homoplastic in the present data set. The sister group (North and South American plus Mediterranean Asidini) is supported by three synapomorphies, but all are relatively homoplastic. These characters need to be examined in a much broader representation of genera, which will probably show that *Craniotus* is derived from the North American Asidini.

The sub-clade of South American tribes (Praocini, etc., stem 32) is supported by



two synapomorphies (24: 1 and 40: 2). The former (mentum and prementum subequal in width) is a reversal; the latter (metendosternite arms fused with mesocoxal inflexions) also occurs in some Coniontini and Asidini. The relatively plesiomorphic nature of these tribes is particularly evident in *Gyriosomus*, in which the elytral-abdominal joint is of the open tongue and groove type found otherwise in flighted species (Char. 79: 2; Fig. 205). In contrast, the internal female tract of *Gyriosomus* is derived (Fig. 132) though clearly of the asidine type.

**Eurymetopine and Tentyriine Clades.** These two clades consistently cluster as sisters with Cnemodini as an outlier, regardless of out-group. The entire assemblage, including Cnemodini is defined by six or seven synapomorphies (Fig. 209, stem 44; Fig. 211, stem 4), and four to six additional synapomorphies define the Eurymetopini plus Tentyriini (less Cnemodini) depending on the out-group. The most important of these are the characters describing the enclosure of the maxillary bases (16: 4; 20: 2; 22: 1; 25: 2). Another character which differentiates this clade from the asidine group of tribes, the style of closure of the procoxal cavities (30: 1; Fig. 32), occurs earlier in the cladogram (stem 40 in Fig. 209). Another distinguishing feature, the presence of dorso-basal mandibular lobes which clasp the labrum (9: 2; 11: 2), is probably a primitive feature of this clade, but occurs sporadically and is of limited diagnostic value.

In contrast, fewer characters, principally features of the ovipositor and internal female reproductive tract, differentiate the eurymetopine and tentyriine clades. Most notably, the form of the internal tract is very different. In Eurymetopini and related tribes the spermathecae arise serially from the base of the accessory gland duct (Figs. 178–180; 183, 184). In the tentyriine group the apex of the bursa is attenuate and often divided into several lobes, (Figs. 195–197), but discrete spermathecae are absent. In the tentyriine group the spiculum ventrale has well developed basal arms (Fig. 203), whereas, in the eurymetopine group the arms are lacking altogether (Figs. 174, 177). The South American tribes Evaniosomini, Thinobatini and Trilobocarini, which do not fit easily into this dichotomy, are discussed at greater length below.

Both the eurymetopine and tentyriine groups are large and morphologically diverse, with much parallelism in specialized body forms. In both groups the more primitive species are winged and in catalogs are included in the same tribe, Epitragini. Other (flightless) genera are adapted for life on or in sand (e.g., *Edrotes*, *Cryptadius*, *Catomulus*, *Oxycara*), with globular bodies and modified forelegs. Another distinctive body form is waisted with long slender legs (e.g., *Triorophus*, *Tentyria*). Such similarities and parallel variation led Koch (1955) to suggest that the New World tribes should be combined under Tentyriini. The results presented here show definitively that the New and Old World lineages are separate, although several of the New World tribes do not merit separate recognition.

A less tractable problem relates to the validity of the relationship of the eurymetopine and tentyriine groups. Despite their high degree of similarity in various features discussed above and their adjacent position in the cladograms, the major differences in configuration of their internal female tracts do not suggest a close relationship. Moreover, no intermediate configurations exist, and it is difficult to envision how one configuration might have become changed into the other. Rather, the eurymetopine system seems obviously related to the arrangement in Cnemodini and Vcronini, while the tentyriine system is similar to the type present in some Stenosini

(e.g., *Grammicus*) or Zophosini (e.g., *Zophosis testudinatus*). If the female tract configurations were considered the defining character, then the similarities in mouthparts, coxal closure and larval body form would have to be attributed to convergence. Related to this problem is the phyletic position of Evaniosomini, Thinobatini and Trilobocarini (discussed below), which have unusual configurations of the female tract not easily derivable from either the eurymetopine or tentyriine group. The cladogram results are accepted as definitive for the present, but the eurymetopine-tentyriine relationship deserves additional study.

The most primitive tribe of the eurymetopine clade is Epitragini. Most Epitragini are winged; all are distinguished from the remaining eurymetopine tribes by the sclerotized and pigmented common duct to which the accessory gland and spermathecae attach (70: 3; Figs. 165, 168–171) and by the configuration of the metendosternite arms (41: 5). The remaining eurymetopine clade is defined by two or three synapomorphies, depending on out-group, but these are subject to high levels of homoplasy and not very convincing. The same is true of the remaining dichotomies defining the eurymetopine tribes (stems 49–52 in Fig. 209), where the synapomorphies involve either loss of wings and concomitant features or characters which are variable within tribes. In particular the use of epistomal configuration and presence or absence or dorso-basal mandibular cusps as tribal characters is unjustified. The epistomum is produced anterad as a prominent lobe in Evaniosomini, Trimytini, Triorophini and Trientomini, but is also developed in many Tentyriini and Eurymetopini. Many genera are intermediate in development of the epistomal lobe, and it may vary considerably in size among closely related species (e.g., *Chilometopon*: Doyen, 1982; *Telabis*: Casey, 1907: 318). The development of dorso-basal mandibular cusps is generally correlated with presence of the epistomal lobe, but many genera with undeveloped epistoma have large mandibular cusps. Of the eurymetopine tribes only Edrotini, which is monogeneric and strongly psammophilous, is easily defined. Triorophini, Auchmobiini, Trientomini, Trimytini and Eurymetopini show morphological intergradation, and tribal assignments of such genera as *Somias*, *Mencheres* and *Posides* appear to be more or less arbitrary. The above tribes should all be combined under Eurymetopini Casey. With this change Eurymetopini and Tentyriini will be approximately equivalent in range of morphological and ecological variation.

Cnemodini Casey, classified near Eurymetopini in catalogs, differs from typical eurymetopine tribes in ovipositor form (Fig. 152; coxites almost as long as paraprocts; apical coxite lobes explanate, upturned), and in configuration of the internal female tract (gland short, compact), and spiculum (Fig. 153; basal arms present). The ovipositor form is similar to that of *Salax* and *Trilobocara* (Figs. 154, 162) and the internal tract is similar to that of the former. *Salax* and *Trilobocara* also have spicula with well developed basal arms (Figs. 156, 163), longer than those of *Cnemodinus*. Various other features of *Cnemodinus* are autapomorphic. For example, the tentorial bridge is absent; the aedeagus and spiculum gastrale are extremely large in relation to body size extending at rest into the metathorax, where they are canted to the right. The median lobe has an unusual, vertically bifurcate apex and the external plates of the spiculum are large, sclerotized and melanized. The position of Cnemodini as an outlier to the combined eurymetopine plus tentyriine clades is due to the lack of dorsal mandibular cusps (Chars. 9: 2; 11: 2). As mentioned above the cusps are



sporadically present throughout both eurymetopine and tentyriine lineages, and were coded as primitively present for both. The absence of cusps in Cnemodini could well be secondary, and changing these two characters causes it to cluster just basal to *Salax*. The position of the latter is discussed at length below. *Salax* and *Cnemodinus* differ strongly in labral and mandibular structure, and Cnemodini should continue to be recognized as a distinct tribe for now.

*Ambigatus* Fairmaire and *Achanius* (treated as subgenera by Kulzer, 1950) are included in catalogs in Evaniosomini, which they phenetically resemble in having slender, elongate bodies. Most species agree closely with Eurymetopini in structure of the internal female reproductive tract (Figs. 179, 180) and spiculum. The former, especially, is strongly differentiated in Evaniosomini. *Ambigatus* and *Achanius* also lack the specialized mandibles of Evaniosomini (Fig. 14). Both taxa should be transferred to Eurymetopini.

The eurymetopine clade occurs almost exclusively in the New World, but in *Ascelosodis*, from the southern Himalayan region, both the internal female tract (Fig. 188) and the spiculum are of the eurymetopine type. In terms of other morphological features *Ascelosodis* agrees with the more generalized Eurymetopini. Probably all species of *Ascelosodis* will prove to be Eurymetopini, and it seems likely that some other eastern Asian genera of Tentyriini may also be Eurymetopini.

The tentyriine clade includes two major Old World tribes, Adesmiini and Tentyriini, which share all important features and are clearly sister taxa. Only one or two synapomorphies shared by the two groups of Tentyriini are absent in Adesmiini, and both are subject to much homoplasy. The more derived genera of Adesmiini are differentiated from Tentyriini by several features. For example, the posterior tentorial arms extend as low ridges to the submentum (6: 2); the anterior margin of the mentum is deeply incised (26: 3); the metendosternite arms are fused with the mesocoxal inflexions (40: 2); the metacoxae are widely separated and much more broadly oval than in Tentyriini (45, 46). In primitive adesmiine genera (e.g., *Aloigenius*, *Epiphysa*; Penrith, 1986b), however, these derived states are often absent. In other cases the derived state also occurs in some derived Tentyriini. Conversely, Adesmiini are primitive regarding enclosure of the maxillary bases (Char. 16), but *Cauricara* has the derived state which is typical of Tentyriini. Most notably, parallel patterns of variation occur in configuration of the internal female reproductive tracts of Adesmiini and Tentyriini (Figs. 196 and 201; 195 and 199). Adesmiini seem to form a single lineage, distinctive in their larger size and generally diurnal habits. Determination of whether tribal recognition of Adesmiini leaves Tentyriini paraphyletic, however, will require a more extensive analysis of tentyriine genera.

The remaining taxa which appear in the tentyriine clade all occur in southern or western South America. *Salax* and *Trilobocara* were treated separately because the aggregate of their characters clearly differentiated them from Trimytini, where they are classified in catalogs. *Achanius* and *Ambigatus*, included in Evaniosomini in catalogs properly belong in Eurymetopini, as discussed above.

Evaniosomini comprise a small group of genera characterized by having compact, locular spermathecae (Char. 65: 2, 68: 4; Figs. 160, 161) rather than the tubular type of Eurymetopini. Thinobatini have the apex of the bursa tapering, smooth and rigid (Fig. 175), similar at least superficially to Tentyriini, but lacking the accessory gland altogether. These structures resemble the spermathecae of Tentyriinae in being poorly

differentiated from the bursa, and received the same numerical code. This is the primary character responsible for their location in the tentyriine clade. However, the obvious differences in spermathecal structure suggest that the three arrangements have arisen independently. The synapomorphies linking Evaniosomini and Thinobatini are primitive (reversals on the cladograms), and these two are probably not very closely related. Besides the obvious spermathecal differences, in Evaniosomini the spiculum ventrale is deeply forked at the base (Fig. 159), whereas in *Thinobatis* it lacks basal branches (Fig. 167), as in the eurymetopine clade.

*Salax* Guérin and *Trilobocara* Solier both have specialized ovipositors with the apical coxite lobes sclerotized, explanate and upcurved (Figs. 154, 155, 162). The spicula are deeply forked at the base (Figs. 156, 163). In the structure of the female tract, however, they are divergent (Figs. 157, 164) and they also differ strongly in the shape of the mandibles and labra. Surprisingly both are fully winged, a condition belied by their stout bodies and relatively short metasterna. These genera fit only very uncomfortably in the tentyriine clade, nor could they be included easily in any existing tribes of the eurymetopine clade. Lacordaire (1859) proposed *Trilobocarides* for this group, and *Trilobocarini* should be resurrected to contain *Trilobocara*, *Salax*, *Megalophrys* Waterhouse, *Eremoeccus* Lacordaire, and *Derosalax* Gebien. *Orthonychius* Gebien is almost certainly synonymous with *Trilobocara*. Evaniosomini should contain *Evaniosomus* Guérin, *Aryenis* Bates, *Evelina* Thomson, *Melaphorus* Guérin, and probably *Chorasmius* Bates, which I have not examined. *Melaphorus* appears under *Triorophini* in the Gebien (1937) catalog, but was placed in Evaniosomini by Peña (1966). Thinobatini should contain *Thinobatis* Eschscholtz and probably *Cordibates* Kulzer, which I have not dissected. *Pseudothinobatis* has the female tract, ovipositor and spiculum as in *Epitragini*, to which it is here transferred.

These South American genera and others such as *Psammetchichus*, *Megelenophorus*, *Aspidolobus* and *Hypselops* display many primitive or aberrant features and need much further study. Association of immatures could be especially valuable for this group.

**Miscellaneous Isolated Taxa** (*Vacronini*, *Lachnogyiini*, *Caenocrypticini*, *Boromorphus*). These taxa either do not belong to the major lineages discussed above or occupy unstable positions.

*Vacronini* appears as an outlier to the combined eurymetopine and tentyriine clades where it clusters with *Zolodinus* and *Lixionica* and sometimes with *Falsomycterus*. Only when *Zolodinus* is declared as out-group does *Vacronini* assume a more basal position on the cladogram (Fig. 211). The relationships of the former genera were discussed at some length earlier, and only *Vacronini* is considered here.

The internal female reproductive tracts of *Alaephus* and *Eupsophulus* (Figs. 147, 150) are both of the eurymetopine configuration with serially arranged spermathecae. They differ from the eurymetopine tribes in both spiculum shape (Fig. 149) and ovipositor configuration (Figs. 146, 148), however, as well as in having completely exposed maxillary bases and internally open procoxal cavities. All *Vacronini* are fully winged. *Vacronini* is best considered an early derivative of the eurymetopine-tentyriine clade. *Lixionica* is tentatively included here, pending discovery of its larva.

The cladistic positions of *Lachnogyia* and *Boromorphus* change drastically, depending on out-group. The female tract of *Lachnogyia* has multiple, serially arranged spermathecae, as in *Vacronini*, but the specialized ovipositor is very different and

the procoxal cavities are internally closed (30: 1). The wings have a strong subcubital fleck and a jugal incision near the hind basal margin. *Boromorphus* has a primitive ovipositor with four distinct coxite lobes and large, apical gonostyli (Fig. 72). The internal tract has a fascicle of four or five short, thin spermathecal tubes attached to the bursa at the base of the gland (Fig. 74). The procoxal cavities are internally closed (30: 1). Both these taxa require tribal recognition, but their relationships cannot be more closely specified at present. I have examined only *Lachnogya squamosa* Menetries and *Boromorphus tagenoides* Lucas. Additional comparisons and especially association of larvae are needed.

Caenocrypticini (Koch, 1958) comprises a small group of genera in southern Africa and *Caenocrypticoides* Kaszab (1969) from the Andean region of South America. Only *Vernayella* represents the African group in this study; *Caenocrypticoides* was examined subsequently and is briefly discussed below. The internal female tract of *Vernayella* has a constricted bursa and small, subspherical accessory gland without separate spermatheca (Fig. 77). This arrangement is similar only to that of some Cnemeplatiini and Stenosini (e.g., *Lepidocnemeplatia*, *Grammicus*). The maxillary bases are exposed, the procoxal cavities are internally closed (30: 3) and the mesocoxal cavities closed by the sternites (34: 2). The ovipositor has the paraprocts and coxites subequal, with the minute gonostyli terminal (Fig. 75). The spiculum (Fig. 76) lacks basal arms. The most unusual feature of these small beetles is the closure of the metacoxal cavities; the metepimeron is exposed posteriorly as a very broad lobe, strongly interlocked with the adjacent abdominal sternite, so that the pterothorax and abdomen form an integral unit (Fig. 37). Analogous interlocking occurs in Cryptochilini and Cnemeplatiini, where the transversely shortened coxae allow the abdominal sternite to interlock with the metasternum.

*Caenocrypticoides* differs from *Vernayella* in internal tract configuration, having a single, coiled spermathecal duct attaching to the narrowed bursa near the gland base. The spiculum has short but distinct basal arms. The metacoxal closure is of the same form as in *Vernayella*, however, and this is their strongest synapomorphy.

Caenocrypticini display a confusing combination of primitive and specialized characters shared with various clades. The larva of *Vernayella* (Endrody-Younga and Doyen, in prep.) has mandibles with an ectal membranous patch, enlarged forelegs and a moderately large tenth sternite. Its most peculiar feature is the minute, apparently closed spiracles. A closed tracheal system was described in *Stenosus* and *Dichillus* by Keleinikova (1976). Because of the larval similarities Caenocrypticini is perhaps best considered as a derivative of the stenosine clade, but more genera clearly need to be examined. *Caenocrypticoides*, based primarily on the metasternal-abdominal interlocking mechanism, appears to be a valid member of this tribe, which is one of only a few pimeliine higher taxa showing vicariance between South America and Africa.

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#### APPENDIX I

Tribes and genera from which the data matrix used in cladistic analyses was derived. Placement of genera within tribes is according to the arrangement of Gebien (1938-1942); tribes and genera are arranged alphabetically.

- Adesmiini: *Adesmia*, *Alogenius*, *Cauricara*, *Epiphysa*, *Metriopus*, *Onymacris*, *Phy-sadesmia*, *Renatiella*
- Akidini: *Akis*, *Morica*
- Anepsiini: *Anepsius*, *Batulius*, *Batuliomorpha*
- Araeoschizini: *Araeoschizus*
- Asidini: *Asida*, *Asidina*, *Asidopsis*, *Cardigenius*, *Heterasida*, *Machla*, *Microschattia*; *Pseudomachla*, *Scotinus*, *Ucalegon*
- Auchmobiini: *Auchmobius*
- Belopini: *Adelonia*, *Belopus*, *Rhypasma*
- Branchini: *Anectus*, *Branchus*, *Oxinthas*
- Caenocrypticini: *Caenocrypticoides*, *Vernayella*
- Calognathini: *Calognathus*
- Ceratanisini: *Ceratanisus*
- Cnemeplatiini: *Actizeta*, *Alaudes*, *Lepidocnemeplatia*, *Thorictosoma*
- Cnemodini: *Cnemodinus*
- Coniontini: *Coelus*, *Coniontis* (including *Coelotaxis*, *Coniontides*), *Conisattus*, *Eusattus*
- Craniotini: *Craniotus*
- Cryptochilini: *Cryptochile*, *Horatoma*, *Pachynoteles*
- Cryptoglossini: *Centrioptera*, *Cryptoglossa*

- Edrotini: *Edrotes*  
 Elenophorini: *Elenophorus*, *Megelenophorus*, *Psammetchus*  
 Epitragini: *Bothrotes*, *Cyrtomius*, *Epitragus*, *Hypselops*, *Lobometopon*, *Nyctopetus*,  
*Omopheres*, *Phegonius*, *Stictoderia*  
 Erodiini: *Apentanodes*, *Erodius*, *Spyrathus*  
 Eurychorini: *Adelostoma*, *Eurychora*, *Herpsis*, *Lepidochora*, *Stips*  
 Eurymetopini: *Ascelosodis*, *Arthroconus*, *Cryptadius*, *Emmenastus*, *Melanastus*,  
*Mencheres*, *Metaponium*, *Stictodera*  
 Evanosomini: *Achanius*, *Ambiguanus*, *Aryennis*, *Evaniosomus*, *Melaphorus*  
 Falsomycterini: *Falsomyxterus*, *Pteroctenus*  
 Lachnogyiini: *Lachnogyia*  
 Molurini: *Brinckia*, *Moluris*, *Phligna*, *Phrynocolus*, *Somaticus*, *Uniungulum*  
 Nycteliini: *Entomochilus*, *Entomoderes*, *Epipedonota*, *Gyriosomus*, *Nyctelia*  
 Nyctoporini: *Nyctoporis*  
 Physogasterini: *Physogaster*  
 Pimeliini: *Lasostola*, *Ocnera*, *Pimelia*, *Sternoplax*  
 Platyopini: *Platyope*  
 Praocini: *Platestes*, *Praocis*  
 Sepidiini: *Sepidium*  
 Stenosini: *Ethas*, *Grammicus*, *Stenosus*  
 Tentyriini: *Anatolica*, *Ascelosodis*, *Asphaltesthes*, *Catomulus*, *Derosphaerius*, *Epitri-*  
*chia*, *Hegeter*, *Himatismus*, *Mesostena*, *Microderopsis*, *Nerina*, *Oxycara*, *Pachy-*  
*chila*, *Rhytinotia*, *Scelosodis*, *Stenosida*, *Scythis*, *Tentyria*  
 Thinobatini: *Pseudothinobatis*, *Thinobatis*  
 Trientomini: *Trientoma*  
 Trimytini: *Chilometopon*, *Salax*, *Trilobocara*, *Trimytis*  
 Triorophini: *Stibia*, *Triorophus*, *Troglogenion*  
 Typhlusechini: *Typhlusechus*  
 Vacronini: *Alaephus*, *Eupsophulus*  
 Vansonini: *Vansonium*  
 Zolodinini: *Zolodinus*  
 Zophosini: *Zophosis* (S.G. *Calosis*, *Cerosis*, *Productylus*, *Zophosis*)  
 Unplaced genera: *Boromorphus*, *Lixionica*, *Idisia*

## APPENDIX II

Brief descriptions of characters and character states. Primitive states designated (p); derived states designated (d), (d<sub>1</sub>), etc. Characters for which the derived states were not ordered are marked with asterisks.

0. Tentorium, bridge: 1. Present (p); 2. Absent or incomplete (d).
1. Tentorium, bridge position: 1. Anterad or in middle of tentorium (Fig. 10) (p); 2. Posterad near occipital foramen (Fig. 11) (d).
2. Tentorium, bridge structure: 1. Slender, subcylindrical in cross section (or absent) (p); 2. Stout, flattened in cross section (d).
3. Tentorium, size: 1.  $\geq \frac{1}{2}$  length gula (p); 2.  $\leq \frac{1}{3}$  length gula (d).
4. Tentorium, position: 1. In posterior half of gular region (p); 2. In middle of gular region (d).

5. Tentorium, configuration of bridge: 1. Looped or strongly arched (Figs. 2, 3, Doyen and Tschinkel, 1982) ( $d_1$ ); 2. Straight or slightly arched (Fig. 11) (p); 3. Angularly bent anterad in middle, or with anteromedial process (Fig. 10) ( $d_2$ ).
6. Tentorium, configuration: 1. Posterior arms remote from submentum (p); 2. Posterior arms extending as separate ridges to submentum ( $d_1$ ); 3. Ridges confluent behind submentum (Fig. 11) ( $d_2$ ).
7. Tentorium, posterior foramen: 1. Broadly open (Figs. 10, 11) (p); 2. Narrowed or closed (Fig. 2; Doyen, 1987) (d).
8. Endocranial septum: 1. Absent (p); 2. Present (d).
9. Right mandible, dorsolateral tooth: 1. Absent (Figs. 13–16) (p); 2. Present, small ( $d_1$ ); 3. Present, large (Fig. 12) ( $d_2$ ).
10. Left mandible, dorsolateral tooth: 1. Absent (p); 2. Present, small ( $d_1$ ); 3. Present, large (Fig. 12) ( $d_2$ ).
11. Mandibles, position of dorsal tooth: 1. On apical half of mandible ( $d_1$ ); 2. Absent (p); 3. On basal half of mandible ( $d_2$ ).
12. Mandible, ventral fossa: 1. Absent (p); 2. Present (Fig. 14) (d).
13. Mandible, prosthema: 1. Present (p); 2. Absent (Fig. 15) (d).
- 14.\* Mandible, form: 1. Retinaculum and mola approximate; prosthema narrow, transverse (or absent) (Fig. 15) ( $d_1$ ); 2. Retinaculum, mola and prosthema "normal" (Figs. 12–14) (p); 3. Mola reduced, attenuate (Fig. 16) ( $d_2$ ).
15. Maxilla, lacinia: 1. Without uncus ( $d_1$ ); 2. With single, simple uncus (p); 3. With bifid or double uncus ( $d_2$ ).
16. Maxilla, articulation of cardo: 1. Concealed in socket in submentum (Fig. 22) ( $d_1$ ); 2. Exposed laterad of submentum (Fig. 21) (p); 3. Concealed in socket overlain by subgena (Fig. 23) ( $d_2$ ); 4. Overlain by both submentum and subgena (Figs. 24, 25) ( $d_3$ ).
17. Postmental region, configuration: 1. Flat, even with subgenae (Figs. 17, 18) (p); 2. Elevated along oral foramen ( $d_1$ ) (Fig. 19); 3. Elevated along foramen and invaginated behind (Fig. 20) ( $d_2$ ).
18. Submentum, form: 1. Continuous with gula posteriorly (Figs. 21, 25) ( $d_1$ ); 2. Distinct sclerite (Figs. 22–24) (p); 3. Reduced, transverse, internal ( $d_2$ ).
19. Submentum, configuration of anterior edge: 1. Pedicellate, produced (Figs. 24, 25) (p); 2. Not produced (Figs. 22, 23) (d).
20. Subgenal processes: 1. Remote from submentum and mentum (Fig. 21) (p); 2. Contiguous with submentum and at least base of mentum (Figs. 22–25) (d).
21. Submental-gular articulation: 1. Submentum adnate to gula, immovable (p); 2. Submentum with slight flexibility against gula (d).
22. Prementum, structure: 1. Entirely membranous ( $d_1$ ); 2. Membranous with basal sclerites (p); 3. Entirely sclerotized ( $d_2$ ).
23. Prementum, position: 1. Entirely exposed anterad mentum; 2. Base concealed beneath mentum (Fig. 28) ( $d_1$ ); 3. Nearly or entirely concealed beneath mentum (Fig. 29) ( $d_2$ ).
24. Prementum, relative size. 1. Mentum and submentum subequal in width (Fig. 28) (p); 2. Mentum expanded, much broader than prementum (Fig. 29) (d).

25. Mentum, shape: 1. Subquadrate (Figs. 21, 24) (p); 2. Much broader than long (Figs. 23, 25) (d).
- 26.\* Mentum, anterior margin: 1. Straight or slightly concave (Fig. 21) (p); 2. Strongly emarginate (Fig. 22) (d<sub>1</sub>); 3. Narrowly notched (Figs. 24, 25) (d<sub>2</sub>).
- 27.\* Mentum, basal articulation: 1. Exposed (Figs. 17–20) (p); 2. Retracted partly beneath submentum, thickened, inflexed (Fig. 26) (d<sub>1</sub>); 3. Concealed beneath expanded submentum (Fig. 27) (d<sub>2</sub>).
28. Oral rim, thickening: 1. Not thickened (p); 2. Thickened behind cardo sockets (d<sub>1</sub>); 3. Thickened behind cardo sockets and mentum (d<sub>2</sub>).
29. Labrum, shape: 1. Subquadrate or slightly longer than wide (p); 2. Distinctly wider than long (d).
30. Procoxal cavity, internal closure: 1. Internally closed (tentoriine closure: see text and Fig. 32) (d<sub>1</sub>); 2. Internally open (p) (Fig. 30, 31); 3. Internally closed (asidine closure, Fig. 33) (d<sub>2</sub>).
31. Procoxal cavity, external closure. 1. Open (Fig. 30) (p); 2. Closed (Figs. 31–33) (d<sub>1</sub>); 3. Secondarily open (d<sub>2</sub>).
32. Procoxal cavity, internal foramen: 1. Undefined (e.g., cavities internally open; Fig. 30) (p); 2. Large, subovate (Fig. 33) (d<sub>1</sub>); 3. Small or minute, sometimes long, very narrow (Fig. 32) (d<sub>2</sub>).
- 33.\* Pro-mesothoracic fusion: 1. Segments freely articulated (p); 2. Edrotine type fusion (see text) (d<sub>1</sub>); 3. Cryptochiline type fusion (d<sub>2</sub>); 4. Nycteliine type fusion (d<sub>3</sub>); 5. Eroidine type fusion (d<sub>4</sub>).
34. Mesocoxal cavity, closure: 1. By mesepimeron (Fig. 5; Doyen, 1987) (p); 2. By sternites (Figs. 36, 37) (d).
35. Mesendosternite, position: 1. Free in haemocoel (p); 2. Horizontal arm fused with anterior rim of mesosternum (d).
36. Mesendosternite, form of dorsal arm: 1. Long, slender, extending at least one third distance to elytral articulation (p); 2. Short or absent (d).
37. Mesendosternite, horizontal arm configuration: 1. Apex attenuate or horizontally flattened (p); 2. Apex expanded as vertical muscle disk (d).
38. Mesendosternite, form: 1. Horizontal portion of arm very short, often oblique (p); 2. Horizontal portion of arm at least half length of dorsal arm, often much longer (d).
39. Mesendosternite, position of dorsal arm: 1. Arising from apex of horizontal arm (or absent) (p); 2. Arising preapically on horizontal arm (d).
40. Metendosternite, form: 1. Arms free in haemocoel (p); 2. Arms fused with mesocoxal inflexions (d).
- 41.\* Metendosternite, configuration of arms: 1. Arms free, apically attenuate (p); 2. Apically fused to mesopleuron at wing process (d<sub>1</sub>); 3. Apically fused with mesotergum (d<sub>2</sub>); 4. With large apical muscle disk, held against tergum by very short muscle (d<sub>3</sub>); 5. With apical muscle disk but not approximate to tergum (d<sub>4</sub>).
42. Metendosternite arm length: 1. Short, ending about at mesocoxal inflexions (d<sub>1</sub>); 2. Extending beyond mesocoxal inflexions about half distance to tergum (p); 3. Long, reaching tergum or nearly so (d<sub>2</sub>).
43. Metacoxal separation: 1. Coxae approximate (p); 2. Coxae separated by at least one coxal length (d).

44. Metacoxa, orientation: 1. Transverse or slightly oblique (p); 2. Oriented at about  $45^\circ$  from longitudinal body axis (d).
45. Metacoxa, proportions: 1. Length (distance between articulations) at least twice width (p); 2. Length less than 1.5 times width (Fig. 35) (d).
46. Metacoxa, lateral enclosure: 1. By metasternum and abdominal sternite 3 (Fig. 35) ( $d_1$ ); 2. By metepisternum (Figs. 34, 37) (p); 3. By sternites and metepisternum (Figs. 36, 36a) ( $d_2$ ).
47. Ovipositor, form: 1. With coxites, proctiger, paraproct and spiculum (Figs. 38, 41, 44) (p); 2. Rudimentary, proctiger, paraproct and sometimes coxites atrophied or lacking; spiculum usually absent (d).
48. Proctiger, length of ventral baculus: 1. Subequal to proctiger (Fig. 44) (p); 2. Much shorter than proctiger (Fig. 166) (d).
49. Gonostyle, position: 1. Terminal or subterminal (Figs. 38, 72) (p); 2. Markedly lateral or preterminal (Figs. 44, 51) (d).
50. Gonostyle, size: 1. Moderate or small, but distinct, digitate or pedunculate with apical seta(e) (Figs. 44, 72) (p); 2. Rudimentary or absent (Figs. 101, 107, 123) (d).
51. Coxite, lobes 3 and 4: 1. With separate sclerites (Figs. 129, 146) (p); 2. Fused (Figs. 51, 84) (d).
52. Coxite, lobe 2: 1. Separate from lobes 3 and 4 (Figs. 107, 120) (p); 2. Fused with 3 and 4 (Figs. 133, 137) (d).
53. Invagination between coxite lobes 1 and 2: 1. Absent (Figs. 60, 72) (p); 2. Present (figs. 44, 63, 129) (d).
54. Apical coxite lobe, texture: 1. Membranous (p); 2. Sclerotized (d).
55. Spiculum, length (as ratio to ovipositor length): 1. Short,  $r < 0.8$  ( $d_1$ ); 2. Moderate,  $0.8 \leq r \leq 1.2$  (p); 3. Long,  $r > 1.2$  ( $d_2$ ).
56. Coxite, baculus basal lobe: 1. Transverse (Figs. 38, 44) (p); 2. Oblique (Fig. 104) (d).
57. Paraproct, extent of apicodorsal lobe: 1. Ending approximately at coxite base (p); 2. Extending  $\frac{1}{4}$  to  $\frac{1}{2}$  length of coxite (Fig. 78) ( $d_1$ ); 3. Extending about  $\frac{3}{4}$  length of coxite (Fig. 104) ( $d_2$ ).
58. Paraproct, position of dorsal baculus: 1. Even with ventral baculus (Figs. 101, 104) (p); 2. Extending proximad much beyond ventral baculus (Figs. 73, 84, 146) (d).
59. Paraproct length (as ratio to coxite length): 1. Proctiger short,  $r < 1.2$  (d); 2. Moderate,  $1.2 \leq r \leq 2.0$  (p); 3. Long,  $2.0 < r \leq 3.0$  ( $d_2$ ); 4. Very long,  $r > 3.0$  ( $d_3$ ).
60. Ovipositor length (as ratio to head length): 1. Short,  $r < 1.0$  ( $d_1$ ); 2. Moderate,  $1.0 \leq r \leq 2.1$  (p); 3. Long,  $r > 2.1$  ( $d_2$ ).
61. Paraproct, extent of ventral lobe: 1. Adjacent to coxite (Fig. 133) (p); 2. Barely overlapping coxite (Fig. 144) ( $d_1$ ); 3. Strongly overlapping coxite (Fig. 137) ( $d_2$ ).
62. Spiculum ( $\varnothing$ ), form: 1. Paired, divergent arms only (Figs. 81, 93) ( $d_2$ ); 2. Forked, with stem and arms subequal in length (Fig. 45) ( $d_1$ ); 3. Forked, stem much longer than arms (Figs. 39, 48) (p); 4. Stem without arms (Figs. 167, 174) ( $d_3$ ).
63. Spiculum ( $\varnothing$ ), form: 1. Arms inclined at about  $45^\circ$  to stem (or absent) (Figs. 45, 127) (p); 2. Arms reflexed (Figs. 105, 118) (d).



- 64.\* Coxite, form of apical lobe: 1. Evenly attenuate, straight (Figs. 107, 137) (p); 2. Akidine type (Figs. 83, 84) (d<sub>1</sub>); 3. Pimeliine type (Figs. 96, 97) (d<sub>2</sub>); 4. Strongly upcurved (Figs. 67, 92, 155) (d<sub>3</sub>); 5. Downcurved (Fig. 78) (d<sub>4</sub>); 6. Weakly upcurved, flat (Fig. 142) (d<sub>5</sub>).
- 65.\* Spermatheca, form: 1. Saccate, unmodified bursa, without separate spermatheca (Figs. 49, 50) (p); 2. Differentiated spermathecal lobe(s) or tube(s) without separate connecting duct to bursa (Figs. 80, 198, 199) (d<sub>1</sub>); 3. Spermathecal tube(s) apical on common duct (Figs. 128, 134) (d<sub>2</sub>); 4. Spermathecal tube(s) lateral on common duct (Figs. 116, 150) (d<sub>3</sub>).
66. Spermatheca, annulation: 1. Nonannulate (Figs. 106, 116) (p); 2. Annulate (Figs. 94, 201) (d).
67. Spermatheca, arrangement of tubes: 1. Multiple, fasciculate tubes (Figs. 86, 135) (d<sub>1</sub>); 2. Single or few fasciculate tubes (or undifferentiated) (Figs. 80, 95) (p); 3. Few serial tubes (Figs. 119, 171) (d<sub>2</sub>); 4. Multiple, serial tubes (Figs. 122, 179, 184) (d<sub>3</sub>).
68. Spermathecal tubes, form: 1. Long, thin, tubular (Figs. 109, 179) (d<sub>2</sub>); 2. Both thick and slender tubes present (Fig. 94) (d<sub>1</sub>); 3. Short, thick (or undefined) (Figs. 43, 74, 89) (p); 4. Locular or capsular (Figs. 40, 46, 62) (d<sub>3</sub>).
69. Spermatheca, form of common duct: 1. Undefined (Figs. 69, 71) (p); 2. Short, thick (Figs. 135, 142) (d<sub>1</sub>); 3. Longer, slender (Figs. 125, 134) (d<sub>2</sub>).
70. Spermatheca—accessory gland common duct, form: 1. Undefined (p); 2. Smooth, flexible, unpigmented (Figs. 140, 183) (d<sub>1</sub>); 3. Rigid, pigmented, annulate (Figs. 165, 170) (d<sub>2</sub>).
71. Spermathecal tube structure: 1. Tubes unbranched; 2. At least some tubes branched (d).
72. Accessory gland duct, form: 1. Straight (or undifferentiated) (Figs. 125, 128) (p); 2. Spiral (Figs. 183, 190) (d).
73. Accessory gland, size: 1. At least twice length of bursa or vagina (Fig. 86) (d<sub>1</sub>); 2. Subequal to bursa, elongate, tubular (Figs. 49, 62) (p); 3. Shorter than bursa, often saccate (Figs. 50, 54) (d<sub>2</sub>); 4. Absent (Fig. 92) (d<sub>3</sub>).
74. Secondary bursa copulatrix: 1. Absent (p); 2. Present (Figs. 150, 164, 165) (d<sub>1</sub>).
75. Spermathecal tubes, configuration: 1. Straight or slightly curved (or absent) (p); 2. Coiled or convoluted (d).
76. Accessory gland, position: 1. Lateral on bursa or vagina, remote from spermatheca (or absent) (Figs. 89, 198, 201) (p); 2. Apical near spermatheca(e) or at its base (Figs. 74, 80, 86) (d<sub>1</sub>); 3. On spermathecal duct (Figs. 116, 134) (d<sub>2</sub>).
77. Abdominal sternites 5 to 7, articulatory membranes: 1. Membranes exposed, external (p); 2. Membranes concealed (d).
78. Flying wings: 1. Present, functional (p); 2. Reduced, brachypterus (d<sub>1</sub>); 3. Absent (d<sub>2</sub>).
- 79.\* Elytral-abdominal joint: 1. Enclosed tongue and groove (Fig. 207) (d<sub>1</sub>); 2. Open trough (winged forms (Fig. 205)) (p); 3. Open tongue and groove (Fig. 206) (d<sub>2</sub>); 4. Amplexiform coupling (Fig. 208) (d<sub>3</sub>).
80. Abdominal laterotergites: 1. Extremely small (d<sub>1</sub>); 2. Moderate (p); 3. Very large, at least on some segments (d<sub>2</sub>).



81. Aedeagus, orientation: 1. Medial lobe ventral to tegmen (p); 2. Median lobe dorsal to tegmen ("inverted") (d).
82. Antennal segment number: 1. Eleven (p); 2. Ten plus reduced eleventh segment ( $d_1$ ); 3. Ten ( $d_2$ ).
83. Antennal form: 1. Serrate-clubbed ( $d_1$ ); 2. Filiform or serrate (p); 3. Serrate-moniliform ( $d_2$ ); 4. Moniliform ( $d_3$ ); 5. Moniliform-clubbed ( $d_4$ ).



## APPENDIX IV Continued.

tree 0 length 734 ci 19 ri 56	
character/steps/ci/ri	
0	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
9	5 3 4 1 9 6 2 2 8 7 5 2 2 3 18 14 7 19
11	20 33 25 100 22 33 50 50 25 28 20 50 50 66 11 21 28 10
33	33 33 50 100 0 0 0 0 71 68 63 0 0 50 27 68 16 32
19	20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37
10	3 3 13 17 9 10 11 4 7 6 17 4 14 4 8 1 10 7
10	33 33 15 11 11 10 18 50 28 16 11 50 14 100 12 100 10 14
40	89 33 64 57 63 64 18 33 81 68 70 33 75 100 69 100 18 33
38	39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56
3	11 10 9 20 11 2 12 8 3 1 12 8 5 10 8 11 13 4
33	9 10 44 10 9 50 8 12 33 100 8 12 20 10 12 9 15 25
83	61 25 37 30 23 0 21 66 50 100 50 46 33 62 66 58 47 0
57	58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
12	12 17 11 2 12 1 13 16 4 21 14 11 9 3 6 17 2 5
16	8 17 18 100 25 100 38 18 25 14 21 18 22 33 16 17 50 20
60	59 53 52 100 57 100 57 70 50 59 76 59 73 0 16 30 0 85
76	77 78 79 80 81 82 83
14	1 10 12 18 1 9 36
14	100 20 25 11 100 22 11
65	100 69 64 40 100 58 23
tree 0 length 761 ci 18 ri 55	
character/steps/ci/ri	
0	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
9	5 3 5 1 9 6 2 2 8 7 5 2 2 3 19 15 7 21
11	20 33 20 100 22 33 50 50 25 28 20 50 50 66 10 20 28 9
33	33 33 33 33 100 0 0 0 0 71 68 63 0 0 50 22 66 16 24
19	20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37
10	3 3 13 18 10 10 11 4 9 7 17 4 15 4 9 1 10 7
10	33 33 15 11 10 10 18 50 22 14 11 50 13 100 11 100 10 14
40	89 33 64 55 60 65 18 33 75 64 70 33 73 100 66 100 18 33
38	39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56
3	12 10 9 20 11 2 12 8 4 1 12 8 6 11 7 12 14 4
33	8 10 44 10 9 50 8 12 25 100 8 12 16 9 14 8 14 25
83	59 25 37 30 23 0 21 66 25 100 52 50 28 60 72 56 45 0
57	58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75
12	13 18 12 2 12 1 13 17 4 21 14 11 9 3 6 17 2 5
16	7 16 16 100 25 100 38 17 25 14 21 18 22 33 16 17 50 20
61	57 50 47 100 57 100 57 69 50 59 77 59 74 0 16 30 0 85
76	77 78 79 80 81 82 83
15	1 12 12 19 2 10 36
13	100 16 25 10 50 20 11
63	100 64 65 37 0 52 23